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May 1912

Editor: JOHN M. COULTER

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THE

BOTANICAL GAZETTE

MAY 1912

RELATIONS OF PARASITIC FUNGI TO THEIR HOST PLANTS

I. STUDIES OF PARASITIZED LEAF TISSUE

ERNEST SHAW REYNOLDS

(WITH NINE FIGURES)

Various phases of pathologic study have occupied the attention of botanists at different times. Before the exciting causes of diseases in plants were known, the general external appearance of the affected organ was described. Later, most of the attention was directed toward the discovery of the parasitic organisms which cause the derangements, and incidentally the study of the physiologic responses of the host was begun. Within the last few years many students of the subject have examined various morphologic changes which occur in diseased plants, first dealing almost entirely with the gross anatomic appearance, but later making more minute histologic and cytologic investigations. Leaf tissue, when invaded by fungi, however, has not been thus carefully studied. Moreover, comparative studies are always helpful in deciding general principles, and so it is in pathologic morphology. Only as we become acquainted with many examples of cytologic and histologic changes, shall we be able to approximate the truth regarding the reaction of the host plant to parasitic invasion. The practical value of such results can hardly be doubted. WOODS (**92**) has written of this matter as follows:

> To most successfully combat a disease, we should know the causes that contribute to it, and as much about the causes as possible. We should under-

stand the pathological reactions of the diseased plant. Only in this way shall we be able to remove the causes or protect the plant against them or assist it to recover.

If, then, we desire to find a safe remedy, we must know all that is possible to know concerning the disease. As a link in the chain of evidence this paper is presented, with the hope that it may serve to extend knowledge of the reaction of leaf tissue to fungous invasion.

Historic

The relations between parasitic fungi and their host plants are of various kinds. The subject might be divided into two parts: (1) the changes in the fungi when grown upon various substrata, and (2) the effects of the fungus upon its host plants. Among the latter we can easily distinguish two classes, though one class is dependent upon the other; those changes which are disturbances of the physiologic processes, and those which are changes in the morphologic structure.

As we are to deal with the latter class in this paper, we shall turn our attention to the investigations on pathologic morphology which have previously been reported. The two phases which we must consider are (1) the anatomic and histologic, dealing with abnormal organs and tissues, and (2) the cytologic, dealing with abnormal cell structures.

Various pathologic modifications of the floral organs have been noted. MOLLIARD (**48**) described various changes in flowers caused by *Peronospora*, *Cystopus*, and other fungi, as well as by insects. WAKKER (**84**), in his most useful paper, reported additionally a number of abnormalities in some or all the organs of various flowers. The reproductive organs and corolla of two species of *Teucrium* are attacked and changed in structure by the larvae of *Copium* (HOUARD **29, 32**). Galls on the flowering parts of *Euphorbia Cyparissias* also were described by HOUARD (**30, 31**). The changes which WARD (**86**) cited as occurring in the buds of *Lilium candidum* are less striking but none the less interesting. The effects of *Cystopus candidus* upon the various organs of its host as described by EBERHARDT (**19, 20**) are notable.

TREUB (**79**) described the effect of *Heterodera* upon the root structure, and other writers have also studied abnormal root structures.

Stems and branches are also subject to invasion by parasites of various kinds. A somewhat detailed description of the deformation caused by *Ustilago* in the stem of *Zea Mays* was given by Miss KNOWLES (**35**), while WAKKER (**84**) showed that many groups of fungi have the power of changing the appearance and structure of stems. The Exoasceae cause numerous hypertrophies and other abnormalities in the vegetative organs as shown by SMITH (**70**). HARTMAN (**27**) described the witch broom of the white fir. Several of our common flowering plants, such as *Hepatica* and certain species of *Euphorbia*, were described by MEEHAN (**43**) as having elongated petioles and stems when attacked by rusts. EBERHARDT (**19, 20**) gave some histologic data regarding various stem tissues in pathologic condition. Some abnormal anatomic conditions were described by MOLLIARD (**50**).

The effects of disease upon the forms of leaves are among the most noticeable of the pathologic phenomena. WORONIN (**93***a*) found various modifications of the leaf tissue caused by *Exobasidium Vaccinii*. *Exoascus* also causes very striking abnormalities in the leaves of various species of *Prunus* that have been described by Miss KNOWLES (**34**), ATKINSON (**4**), and SMITH (**70**). WAKKER (**84**) described various leaf modifications due to fungi. Some histologic changes of the needles of the witch broom of the white fir were noted by HARTMAN (**27**). The observations of PEGLION (**63**) showed that other kinds of rusts cause changes in the structure of leaves and stems. The anatomic changes caused by species of *Gymnosporangium* were described by WÖRNLE (**94***a*); and ANDERSON (**1**) described the same for *Aecidium elatinum* on *Abies balsamea*. Plants growing normally in one range of temperature, when placed in a colder climate are often noticeably affected. BONNIER (**6, 7**), WAGNER (**83**), and HOUARD (**28**) have given us valuable results in their studies on this subject. Intumescences caused by abnormal environment have been described by Miss DALE (**13, 14, 15**), VON SCHRENK (**67***a*), and others. The effects of various chemical substances upon plants have been studied. Of the work on this

subject we may mention that of WILFARTH and WIMMER (**89, 90**), CROCKER and KNIGHT (**12**), NĚMEC (**59**), and ANDREWS (**3**). Finally, we may note that wind has been found to play an important part in the production of abnormalities. Such observations were made by HANSEN (**26***a*) and BRUCK (**9**). The general subject of "pathological plant anatomy" has been most satisfactorily reviewed by KÜSTER (**38**), who has also published various articles upon various phases of the subject, but especially concerning the anatomic features of gall tissues (**37**). This review of papers upon the subject of the histologic and gross anatomic changes, though incomplete, will serve to show the present extent of the subject, and through these references the rest of the papers may be traced.

From the following review of work upon pathologic cytology it will be seen that fungi, insects, poisonous substances, changes of temperature, and other physical forces all tend to modify the plant cell.

WORONIN (**93***a*) found that *Exobasidium Vaccinii* on *Vaccinium Vitis-Idaea* reduces the amount of chlorophyll, and that the red-colored erythrophyll takes its place in the palisade cells. Miss KNOWLES (**34**) found that when peach leaves are attacked by *Exoascus deformans* the epidermal cells become rounded and have thickened walls, the palisade cells become nearly isodiametric, and the protoplasm is reduced in amount. ATKINSON (**4**) found that certain of the parenchyma cells become "very much elongated and curved or sinuous in form." TUBEUF (**80**) mentioned secondary cell formation in the palisade of *Populus niger* in leaves attacked by *Exoascus aureus*. In the cells of *Lilium candidum* affected by a *Botrytis* disease, WARD (**86**) found that the mycelium causes a swelling, dissolving, and discoloring of the cellulose cell walls, but does not directly affect the protoplasmic parts. The same observer (**87**) described similar effects of a *Botrytis* disease upon the snowdrop. In WAKKER'S paper (**84**) there are occasional references to cytologic phenomena. In most of the hypertrophied parts no chlorophyll is formed. Calcium oxalate is in the form of masses of small crystals ("Drusen") in the flower and leaf cells of *Rhamnus Frangula*, but is wanting usually in the parts attacked by *Aecidium*. In other cases numerous small individual crystals

are formed. Starch is often abundant in certain hypertrophies. Bacteria were reported by DANGEARD (**16, 17**) as causing the swelling of the nucleus of *Euglena*, the disappearance of the nucleolus, and the disorganization of the chloroplasts. The effect on the contents of cells in the process of fermentation has been studied by MATRUCHOT and MOLLIARD (**46**), and PEIRCE (**64***a*) has described the changes in the root tubercles on the bur clover. *Cystopus candidus* usually causes an unusual deposition of starch and formation of chlorophyll in parts usually free from these substances, as described by EBERHARDT (**19, 20**). Other students, as GRANT SMITH (**69**), NORDHAUSEN (**61**), W. G. SMITH (**70**), WÖRNLE (**94***a*), HALSTED (**25***b*), MIYOSHI (**44***b*), and HARTIG (**26***b*), have noted the effects of fungous invasion upon the cellulose walls, and the distribution of starch and of calcium oxalate. The cellulose walls may be thickened or dissolved, and the starch and calcium oxalate content may be increased or decreased as determined by the season, the specific invader, and the host. WARD (**88**) has found that in the wheat plant the hyphae of the invading rust do not seem to affect the "chlorophyll-corpuscles or the nuclei until a late stage of growth." The leaves of the witch broom of the white fir are described by HARTMAN (**27**) as having small amounts of chlorophyll and starch. WÖRNLE (**94***a*) reports that *Gymnosporangium* causes excessive nuclear division and cell formation in pine needles. The Ustilagineae, according to STROHMEYER (**75**), cause various changes in the cells of the host, both hypertrophy and hyperplasy of the parenchyma occurring. MOLLIARD (**48**) described a number of cytologic changes caused by insects and fungi growing on various hosts. *Cystopus candidus* causes the cells to assume abnormal forms and sizes, the nuclei to enlarge, and the normal chlorophyll content to change. *Peronospora* does not affect its hosts in this way. *Puccinia Violae* on *Viola silvestris* causes the nuclei and the nucleoli to enlarge, and the power of division of the former to increase. The petals of *Euphorbia Cyparissias* when attacked by *Uromyces scutellatus* and *U. praeminens* show cells with enlarged nuclei and chlorophyll formation.

The effects of various insect parasites upon the vegetative cells may be summed up in general thus: nuclei and nucleoli

enlarged, chloroplasts reduced in size, often a more abundant protoplasm than normally, and variations in the calcium oxalate content. In some fungous galls GUTTENBERG (**24**) found a tendency for the nucleus to become lobed, to divide amitotically, to decrease in size, and to force the chromatin toward the periphery. The cytologic features of some gall tissues, resulting from insect invasion, has also been described by MOLLIARD (**49**). The nuclei show a decided tendency toward amitotic division, which often results in the presence of several nuclei in a cell, with no formation of new walls. The nucleoli as well as the nuclei become greatly hypertrophied, and the former may be divided often without the subsequent division of the nucleus. At times the nucleus multiplies by a method of budding in addition to the more common means of abstriction. The nuclear membrane may finally disappear, and eventually even the nucleoli may become disintegrated. HOUARD (**29**) reported similar hypertrophy of the cell organs of the flowers of *Teucrium* when attacked by the larvae of *Copium*. PERCIVAL (**64***b*) described the effect of *Synchytrium* in the potato "wart disease" upon the host cells. These enlarge, the cytoplasm increases, and the nucleus becomes deformed. "The organisms stimulate the invaded cells and at the same time appear to stimulate division and growth in the adjoining cells." Changes in root cells have been noted from time to time, especially in the studies on mycorhizae. MAGNUS (**41**) found the nucleus modified in these symbiotic structures. SHIBATA (**68**) notes that the nuclei in such conditions become enlarged, amoeboid, and divide amitotically. They may be strongly colored at first, but later they seem to become normal as regards division and color. ZACH (**94***b*) describes the following cytological changes in cycad root cells due to fungous invasion. The nucleus becomes amoeboid or otherwise misshapen, the starch is dissolved away, the calcium oxalate increases in amount, and finally nucleus and plasm die. The cells of the growing point and the *Anabaena* region are not seriously invaded. MOLLIARD (**52**) reported that the nematode worm lives in a tissue which has giant cells with numerous nuclei and enlarged nucleoli. VUILLEMIN and LEGRAIN (**82**) reported various nuclear phenomena caused by the same worm in symbiotic relationship with the roots

of plants cultivated in the dry Sahara region. MOLLIARD (**51**) found "nuclear protoplasmic division" in stems attacked by *Phytoptus*. NAWASCHIN (**54**) described strongly hypertrophied cells, and enlarged nuclei with poor chromatin content, in tissues invaded by *Plasmodiophora Brassicae*. TOUMEY (**77**) noted that the nucleus of a crown-gall cell becomes much enlarged and finally "appears as if eroded on the surface." The nucleoli are very persistent. Under abnormal conditions the root tip of *Allium Cepa* shows enlarged cells and nuclei (some lacking nucleoli), and often an increased amount of chromatin. NĚMEC (**56**) also noticed nuclear fragmentation in the same root tips. The nuclei in leguminous root tubercles are reported by PARATONE (**62**) as becoming amoeboid and abnormally colored; CHODAT (**11**), however, noted no great changes.

The effects of changes of temperature upon cell structure have also been studied to some extent. PRILLIEUX (**65**) grew seedlings in heated soil, and found that the nuclei became numerous and variable in form. They increased by fragmentation and often possess numerous nucleoli of various shapes and sizes. These are vacuolated. NĚMEC (**57**) found that nuclei assume amoeboid forms in lowered temperatures. SCHRAMMEN (**66**) found that abnormal nuclear division ("pseudomitosis"), abnormal size of nucleus, and abnormal mass of nucleolin and kinoplasm resulted from changing the temperature surrounding the growing point of a *Vicia Faba* stem. MATRUCHOT and MOLLIARD (**45, 47**) give very detailed descriptions of abnormal nuclei produced at freezing temperatures, especially noting the distribution of chromatin. NĚMEC (**58***a*) produced multinucleated cells in the roots of *Vicia Faba* by placing them in a 1 per cent copper sulphate solution; upon returning them to normal conditions karyogamy took place and uninucleated cells were formed. GRANT (**23**) has reported upon various multinucleated cells. ANDREWS (**2**) found that a nucleus, deprived of its nucleolus can survive for a long time, but a new nucleolus is not formed. The influence of benzene gas upon cell formation was studied by BLAZEK (**5***a*), who reported that simultaneous nuclear division takes place, and many daughter nuclei are formed either with or without subsequent cell wall

formation. WASIELEWSKI (**85**) and WISSELINGH (**91**) have discussed the question of amitosis in various tissues. Miss DALE (**13, 15**) found that in certain intumescences caused by abnormal light, heat, etc., oil is formed in place of starch, the nuclei become club-shaped and highly refractive, and the nucleoli are often increased in number. Amitosis was found to be almost universal, and formed nuclei of unequal size. VON SCHRENK (**67***a*) described similar intumescences due to chemic stimulation. Other studies upon the structure of intumescences were made by SORAUER (**71, 72**) and STEINER (**73**). The structure and the pathologic modifications of chromatophores have been studied by KÜSTER (**39**) in *Ceramium* cells, where under various influences they may be contracted into drops or flattened out into irregular bands. NĚMEC (**55**) has reported the decrease in the number of chromosomes in old tissue, and their increase in hypertrophied cells. Besides these already enumerated, it would be well to note the following as articles dealing with several phases of the subject, and containing valuable lists of references: ZIMMERMAN (**96, 97**), WARD (**87**), UNGER (**81**), FAIRCHILD (**21**), and NĚMEC (**60**). Some abnormal nuclear phenomena have been described also by MIEHE (**44***a*) near wound tissue, KOHL (**36**) in cells under the influence of asparagin, and ZACHARIAS (**95**) under various influences.

Summing up the results so far obtained in the study of the effects of parasitic invasion and abnormal physiologic influence upon the histologic and cytologic elements of plants, we find that the various kinds of tissues, collenchyma, parenchyma, sclerenchyma, and cork, may be abnormally developed or repressed; cell walls may be simply perforated, or much thickened and more or less changed in constitution; secondary cell formation may arise; nuclei and nucleoli may be increased or reduced in number and size, and variously deformed; chromatin may likewise be increased or decreased; the cell sap may acquire a new color; the starch and calcium oxalate content may change; and the chromatophores changed in appearance and efficiency.

Methods

For the investigations to be reported here the ordinary methods of preserving the material were used. The medium solution of

chromacetic acid was found to be the most useful killing and fixing fluid experimented with. Picric alcohol was less satisfactory, because stains of several kinds refuse to affect the tissue when preserved in this solution. For the same reason, picronigrosin was not very successful. An abundance of material was usually kept in the dry condition as herbarium specimens, and some was preserved as well in 4 per cent formalin. Paraffin, melting at about 52° C., was used for most of the work, though the harder grade, melting at 60°, was employed for some of the tough, resistant leaf tissues.

The orseillin-anilin blue method of staining, as outlined by STRASBURGER (**74***a*), was used for all of the preliminary work. This combination serves to differentiate the fungus in the host tissue, and also to make it easy to distinguish the cell contents. The latter stains rather darkly with orseillin, and the host cell walls lightly with the anilin blue. The fungous walls stain much more deeply with the anilin blue. Later in the work, when studying the nucleus, Haidenhain's hematoxylin was used, about as outlined by CHAMBERLAIN (**10**). The differentiation thus obtained was very satisfactory, since the nucleus held the stain more tenaciously than did the cell walls. Fuchsin also was used to some extent.

About 50 different specimens were preserved, sectioned, and examined. Many of these failed to be of value, either because of the great destruction of the host tissue by the fungus, or because of the absence of distinctive and recognizable cytologic changes. The drawings were all made with a camera lucida; and a $\frac{1}{12}$-inch, achromatic oil immersion objective was used for all high magnifications in all camera drawings. The drawings, with one or two exceptions, are of the same magnification, and hence can be compared directly with one another. The attempt was made to get satisfactory material which would illustrate as great a diversity of host plants as well as of fungi as possible. In the following pages, therefore, there will be representatives of both monocotyledons and dicotyledons, and of the latter from several diverse families. The Uredineae, the Ustilagineae, the Phycomycetes, and the Fungi Imperfecti are all represented. The descriptions

of normal and diseased material are from the slides prepared by the methods above mentioned. The normal tissue was cut from the same leaf as the diseased, unless the leaf showed in all parts the effect of the parasitism. In this case a leaf close to the diseased one was chosen in order to have comparable material.

Observations

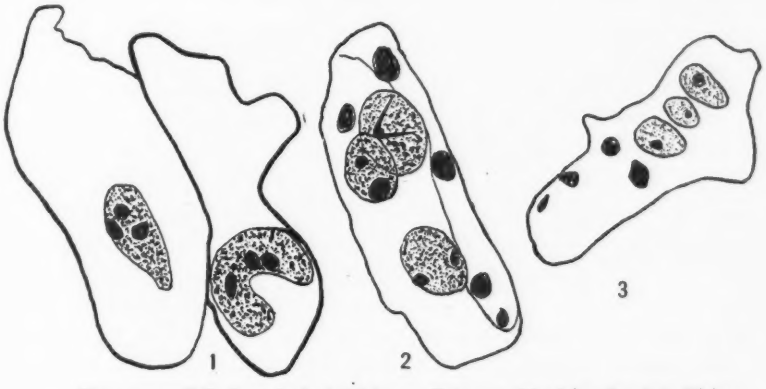
1. GAYLUSSACIA BACCATA (Wang.) C. Koch.—The cause of the disease is not clear. The diseased area is blackest on the upper side, and a white deposit is found on the lower surface of the leaf. The normal leaf tissue is as follows: (1) a single layer of nearly isodiametric cells in the upper epidermis; (2) a single layer of palisade cells; (3) a rather loose, spongy parenchyma with comparatively large intercellular spaces; and (4) a lower epidermis of cells usually somewhat smaller than those of the upper epidermis. The plant studied was collected in early summer, and hence the leaves were fully formed, but still in a vigorous condition. The location of the plant was at the edge of a wooded area, but open, so that the leaves received an abundance of light. The leaf cells have a thin peripheral lining of protoplasm, in which the chloroplasts and the nuclei are imbedded. The cuticle is nearly colorless, and much thicker over the upper than over the lower epidermal cells.

The parasitized leaf shows a number of changes. Just before the palisade cells and after the sponge cells begin to collapse, they are filled with a uniformly brown-stained material. Previous to this they are filled with a granular mass which is stained yellow-brown. In both of these stages of degeneration there are neither chloroplasts nor nuclei to be seen. At the same time, the upper epidermal cells become considerably elongated, and the cuticle is light yellow to brown. In the last phase of degeneration the epidermal cells become completely collapsed, the palisade cells are much shrunken, and the sponge cells have practically disappeared, while the cell walls are uniformly brown, and the cells empty.

2. VIOLA CUCULLATA Ait. (?), parasitized by *Puccinia Violae* (Schum.) DC.—The normal leaf tissue of this plant is rather poorly differentiated. The epidermal cells are very irregular in shape and size, and the cuticle is thin. The mesophyll is composed of a loose

mesh of rounded cells, stretching from one epidermis to the other. The tissue is evidently very easily ruptured, and is seldom complete except at the veins and in connection with the fungous spore beds. The plants examined were growing in a well-shaded and damp location, and were collected in early summer.

In the parasitized regions the cells are closely compacted, and more or less bound together by the invading mycelium which fills the intercellular spaces. Here also the hematoxylin stains much more intensely than in the normal tissue. There seems to be some hyperplasy of the mesophyll. The epidermis is ruptured by the



FIGS. 1–3.—Cells from leaf of *Viola cucullata* parasitized by *Puccinia Violae*: fig. 1, two cells showing deformed nuclei and increased number of nucleoli; fig. 2, cell showing three nuclei and a few chloroplasts; fig. 3, cell showing three deformed nuclei.

spore bed, but the influence of the fungus does not extend far beyond this radius. The nuclei, which are not prominent in the normal cells, become somewhat enlarged, and increase in number in the cells. There are numerous instances where the number is increased to two, while some cells were noticed that contained three nuclei. The nuclei are also more or less deformed, varying from nearly circular in cross-section to oval, oblong, or slightly pear-shaped. The chloroplasts seem to be little affected, at least in shape and size, by the presence of the parasite. Fig. 1 shows some examples of the deformations to the nuclei which are found in the cells near the

spore bed of the rust; fig. 2 shows the abnormal number of three nuclei in one cell; while fig. 3 shows some deformation accompanying the hyperplastic condition.

3. PSEDERA TRICUSPIDATA (Sieb. and Zucc.) Rehder, parasitized by *Phyllosticta Labruscae* Thum.—The normal leaf tissue is similar to that of the *Gaylussacia* described above, and the pathologic changes are very much alike in the two plants. The browning and collapse of the epidermal, palisade, and sponge cells are common to both. The early disappearance of nuclei and chloroplasts is also similar in the two. There is in this case a granular protoplasm in the cells next to the dead area, while the homogeneous brown mass is not formed. The sponge tissue is more completely disorganized than the palisade. This plant, collected in early July, was growing upon a wall exposed to the morning sun.

4. SMILAX GLAUCA Walt., parasitized by a member of the Phaeodidymae of the Sphaerioidaceae.—The leaf parenchyma is not differentiated into palisade and sponge tissues. The diseased area is badly shrunken and broken down. The fungous perithecia are scattered irregularly over this dead area. Because of the thorough killing of the host tissue, no special cytologic changes could be noted. At the edges of the diseased area the cells of both the upper and lower epidermis are turned brown to black, while some of the mesophyll cells are filled with a uniformly brown-staining material. The intercellular spaces and the primary lamellae are often stained very deeply by the hematoxylin. In this transition region no cell organs are visible, and whatever is left of the protoplast is turned black or brown. This coloration sometimes extends to the cell walls as well.

5. POTENTILLA CANADENSIS L., parasitized by *Puccinia Potentillae* Schw. (?).—There is a double parasitism represented here. *Darluca filum* was found growing abundantly upon the spore beds of the rust, and at times apparently directly upon the leaf tissue of *Potentilla*. This latter condition, however, may have been due to the rust mycelium in the tissues which had not yet produced a noticeable spore bed.

The normal structure of this *Potentilla* leaf is somewhat more complex than that of the *Viola* described previously. The palisade

cells have a more oblong longitudinal section than the sponge cells and are more closely packed. The plants collected were growing in a place which was shaded all of the afternoon and part of the morning. The collection was made about the middle of July.

When the leaf is attacked by the rust, the epidermis is broken, the palisade is poorly developed, and more or less replaced by rounded cells common to the sponge and the diseased palisade tissues. In the early stages of the disease the epidermis separates from the mesophyll. There is some hyperplasy of the sponge tissue. The cells, which remain in the tissue directly under the spore beds, are widely scattered and separated by the mycelium of the rust. When the rust is parasitized by *Darluca* the palisade tissue is less abnormal and disorganized. The chlorophyll seems to have largely disappeared from the cells which are within the influence of the rust. A similar effect upon the nuclei is usually seen. An increase in the number of nuclei in individual cells was noticed, however, in tissue just below a perithecium of *Darluca*, which was found imbedded directly in the tissue of the *Potentilla* leaf. Fig. 4 shows two contiguous cells, each having two nuclei; there is also a distinct deformation of these double nuclei.

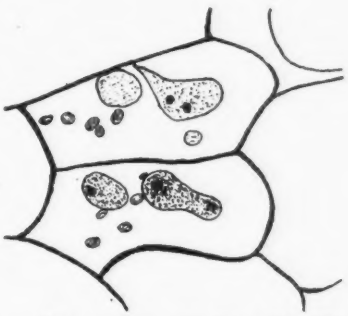
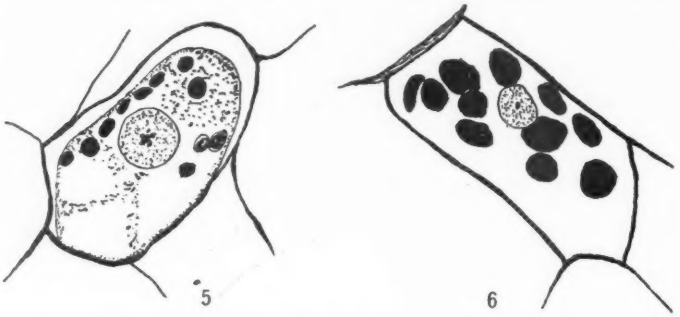


FIG. 4.—Two cells from *Potentilla canadensis* leaf parasitized by *Puccinia Potentillae*, showing two nuclei in each, and in one a suggestion of the beginning of an abnormal division of one of the nuclei.

6. PANICUM LATIFOLIUM L.—The cause of the disease upon this *Panicum* is not clear, though it is surely of fungous nature. The normal leaf tissue is that of the ordinary grasses. The epidermal cells on both sides of the leaf are very large as compared with the simple mesophyll cells which occupy the space between the two layers of epidermis. In the healthy chlorophyllose cells there is only a thin peripheral lining of protoplasm in which the nuclei and the chloroplasts are distributed.

Many of the cells of the diseased area are filled with a homogeneous substance which stains blue, so that at a glance the location of the diseased tissue can easily be discovered. The protoplasm, which is somewhat more abundant and more evenly distributed in the diseased cells than in the normal, is very finely granulated. Many of the diseased cells show two nuclei. All of the nuclei in the vicinity stain deeper or retain the stain more tenaciously than in the healthy tissue, and are relatively larger than in the normal cells. The chlorophyll has largely disappeared from the cells close to the point of invasion, but farther away the



FIGS. 5, 6.—Cells from leaf of *Panicum latifolium:* fig. 5, cell from a diseased leaf, showing an enlarged nucleus and diminutive chloroplasts; the cell is slightly plasmolyzed; fig. 6, cell from an unaffected region, showing a normal nucleus and normally sized chloroplasts.

chloroplasts are merely reduced in size. Figs. 5 and 6 show enlarged and normal nuclei respectively; the difference in the size of the chloroplasts is easily seen also.

7. PYRUS MALUS L., parasitized by *Gymnosporangium* sp.—The structure of this leaf is somewhat more complex than any of those previously described. The upper and lower epidermal cells are in single layers, and are partly isodiametric and partly oblong in shape. The palisade cells, which are in two layers, have their nuclei symmetrically placed in the peripheral protoplasm close to the middle of the lateral walls. The chloroplasts are also arranged along the same walls. The cells of the upper palisade layer are about a third longer than those of the second layer, and are about the

same width as those cells. This palisade occupies half the thickness of the leaf. The sponge cells are loosely connected and have large air chambers scattered among them. The tree, from which the diseased leaves were taken, was growing in a thicket, and about 50 feet from a *Juniperus* tree.

The portion of the leaf which is parasitized is about twice as thick as the normal tissue. This thickening is due to two factors, the hypertrophy of the sponge tissue, and the presence of masses of mycelium. The palisade cells are least affected. The cells in the upper layer are shortened until they are about the length of the cells in the second layer. The space thus left between the upper epidermis and the palisade cells is occupied by mycelium from which the pycnia are developed. The upper epidermis is puffed up and ruptured, the cells are nearly collapsed, the walls are changed to a brown color, and the cuticle is mostly destroyed. The parenchyma cell walls seem to remain about normal. The sponge cells are enlarged to twice or thrice their normal diameters, and the spaces between are filled with the heavily stained mycelium. The nuclei of the sponge cells are the first to show the effects of the presence of the fungus by becoming rather larger than they are normally. They are not, however, otherwise materially changed. Many cells are partially filled with a yellow, granular deposit (fig. 7).[1]

FIG. 7.—A diseased cell from a leaf of *Pyrus Malus* parasitized by *Gymnosporangium*, showing no contents except irregular yellowish granules.

8. SMILACINA RACEMOSA (L.) Desf., parasitized by *Phyllosticta cruenta* (Fr.) Kicks.—The leaf of *Smilacina* is rather simple in structure. The upper epidermis has relatively large oblong cells, interspersed at intervals with short cubical cells. The lower epidermis has smaller and usually more regular cells. Between these two layers is a rather loose parenchyma with large air spaces, and with the larger number of cells close to the upper epidermis. The plants collected were growing at the side of a road through the woods, where the light was rather weak and there was abundant moisture.

[1] Fig. 7 was drawn with a $\frac{1}{8}$-inch objective, and hence is not on the same scale as the other figures.

In the diseased area the cuticle and the epidermal cells are affected to a greater distance from the center of infection than the sponge cells. They are early turned brown and the epidermis is shrunken. The sponge tissue is badly disorganized, but chloroplasts and nuclei are present. The latter attain a larger size, and have a light brown color, whereas when normal they are easily stained with hematoxylin. They often have two nuclei and a granular plasm. Later, in the degeneration of the nucleus, the nucleoli disappear and the nucleus stains deeper. The chloroplasts may later disappear and afterward the other constituents of the cell. Fig. 8 shows the light brown enlarged nuclei in cells affected by the parasite.

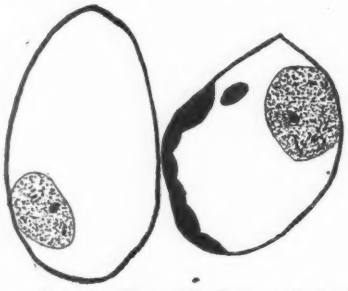


FIG. 8.—Two cells from a leaf of *Smilacina racemosa* parasitized by *Phyllosticta cruenta*, showing enlarged nuclei.

9. CASTANEA DENTATA (Marsh.) Borkh., parasitized by *Cryptosporium epiphyllum* C. and E.—The normal leaf is covered by an epidermis with cells rather larger than those of the sponge tissue. The palisade tissue, which is composed of very long narrow cells, sometimes with a row of short cells below, occupies about half of the total thickness of the leaf. The sponge is very loose and has large air chambers. The cells of the lower epidermis are smaller than those of the upper.

As examined in prepared material, the diseased area is very sharply separated from the healthy part of the leaf. There are practically no cells that show transition phases between the normal and the diseased conditions. The epidermal cells over the parasitized portion are flattened, and often filled with granular deposits which have also been noticed in other diseased plants. The palisade and sponge cells are much shrunken and the entire contents were killed apparently before the specimen was collected. The entire diseased area is yellow-brown, while the normal tissue stains easily with anilin blue. No cytologic changes are to be seen except the deposit of the yellow-brown material throughout

many of the cells, and the occasional enlargement of the nucleus. In some cases the palisade tissue has thus been affected, while the sponge cells are less noticeably changed.

10. XANTHIUM CANADENSE Mill. (?), parasitized by *Puccinia Xanthii* Schu.—The normal leaf tissue is very loosely formed between the upper and the lower epidermal layers. The palisade is scattered, and the sponge is permeated by very large air chambers. Transitional phases between the normal and the diseased conditions of the host cells were not found.

This tissue is more profoundly altered than any other under discussion. It is in many places almost completely replaced by the fungous mycelium. The cells which remain have no protoplasm and are filled with oil globules. On both the upper and the lower leaf surfaces the mycelium is abundant and the telial spores are very numerous. Within the mixture of parenchyma cells and mycelium, which replaces the normal tissue, there are cystlike bodies which are composed of masses of mycelium. These objects are hollow spheres, and from the inner surface arise telial spores exactly similar to those borne in the normal way upon the exterior of the leaf. Part of the mycelium near the exterior stained brown, while that within the host tissue stained blue with anilin blue.

11. ZEA MAYS L., parasitized by *Ustilago Maydis* (DC.) Tul.—The normal host cells are not changed in general appearance, and the general structure of the leaf remains practically normal. Very early in the disease the chloroplasts disappear, but the nuclei remain until very late in the formation of the spores by the smut. In some cases the number of nuclei in a cell is increased, two being the largest number noticed. In this condition the nuclei may also be slightly reduced in size. The nuclei often become deformed, varying from globular to pear-shaped or even crescent-shaped. This deformation seems to be due to mechanical forces at least in part, for in the first place there are cases in which the nucleus is pressed upon on all sides by the forming spores, and the nucleus conforms itself to the rounded shape of the spore walls; in the second place there are nuclei in the diseased area and even in the cells being filled with spores which are normal in shape. If the deformation were due to chemic stimulation, this latter condition

would hardly obtain. The epidermal cells over a diseased region are often filled with a yellowish granular deposit. In the diseased area the cells of the vascular bundle and of the parenchyma alike become filled with a uniform gray plasm, which later breaks up into rounded or hexagonal areas as shown in fig. 9. In the latter stage of the disease these attain more clearly defined walls. It seems evident that these develop eventually into the fungous spores, though the material at hand was not quite old enough to show the last stage of the transformation into the spores. No mycelium was found in the diseased tissue after the formation of the areas mentioned above had begun. It would seem from this that after a certain stage in the disease the fungous mycelium passes into a plastic stage within the host cells, and that then the plastic mass breaks up into spores as previously described. Miss KNOWLES (**35**) states, in her study of the effect of this same fungus upon the corn stem, that the vegetative mycelium breaks up into masses of smaller filaments which swell up, "except that in many cases, indeed in most cases, the filaments lose their individual form and are more or less blended in a gelatinous, shapeless mass." This gelatinous mass fills the host cells at least in the leaf tissue.

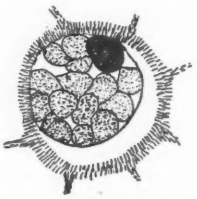


FIG. 9.—One of the outer elements of a vein in a leaf of *Zea Mays* parasitized by *Ustilago Maydis*, showing nucleus and early stage in spore formation within the cell.

12. RAPHANUS SATIVUS L., parasitized by *Albugo canadensis* (Pers.) Kuntze.—The fungus was growing on the cotyledons of young seedlings which were grown in the greenhouse. There is no regular structure to the parenchymatous tissue, as it is all of the ordinary sponge type. There is apparently no great hypertrophy or hyperplasy of the tissues. The blisters seem to be caused by the formation of the mycelium, conidiophores, and conidia just below the epidermis. Few, if any, changes in the cell organs are to be seen. The mycelium is found in abundance. The effect of this fungus seems to be merely that of starvation of the host, not that of poisoning it.

Discussion and conclusions

The changes which are caused in leaf tissue by parasitic fungi are similar to those which have previously been reported as occurring in other parts of phanerogamic plants, and caused by insect invasion, changes of temperature, and parasitic fungi. A comparison of the observations reported in the latter part of this paper with those of other workers reviewed in the earlier part will show that the enlarging, changing of form, and dividing of the nucleus, the changing of the composition of the cell walls, the reduction in the amount of chlorophyll, and other changes in the normal content of the leaf cells are all duplicated in other organs affected by destructive agents.

These changes are usually only variations of natural processes, and are not phenomena that are known only in pathologic tissues, for it is to be noted that these changes in the appearance of the nuclei are not unknown in normal vegetable cells. JOHOW (**33**) describes amitosis as occurring in the older cells of *Chara foetida*. The presence of two or more nuclei in a cell has been noted by TREUB (**78**) in bast cells of various plants; while a process of division is reported by VON BRETFELD (**8**) and MASSART (**42***a*) as so common in wound tissues that they believed nearly all such tissue is formed by the "amitotic" process, as they called it. More detailed work is necessary to show whether the amitotic process of JOHOW and the processes of nuclear division in wound and disease tissues are really analogous, since the former process seems to be for the purpose of increasing the nuclei in connection with the metabolism of mature cells, and the latter processes often lead to an increase in the number of cells, and are found in cells apparently stimulated to a kind of rejuvenescence. SCHÜRHOFF (**67***b*), moreover, has shown that this idea is far from correct, since there are many cases of mitosis in wound tissue, and no true amitosis is certainly known in these tissues. A process that appears to be true amitosis has been reported by SHIBATA (**68**) in mycorhizal cells, and by TISCHLER (**76**) in *Heterodera* galls on *Circaea*. A rather detailed discussion of this question is given by Miss DALE (**15**); while KÜSTER (**40**) and STRASBURGER (**74***b*) review the whole subject of the direct and indirect methods of nuclear division.

No nuclei were noted in actual process of division, but in a few instances there is some evidence of abnormal division. In *Potentilla* (fig. 4) such is the case. The nucleus is somewhat elongated, and at one end is stretched out into a conical point. A comparison of fig. 4 with HÄCKER'S (**25***a*) figs. 9, 10, 14, and 16 will show the close resemblance between the nuclei supposed to have divided recently (fig. 4) and the actual process as reported by HÄCKER. A case which is less clearly related is seen in fig. 1, where the nucleus is pear-shaped. Whether or not these are cases of true amitosis or of pseudoamitosis could not be determined, as only the end products were seen.

The composition of the cell walls of the host may be changed. Two evidences of this are forthcoming. In *Panicum*, especially, it was noted that the walls of the parasitized cells are more deeply stained than those of the ordinary cells. Since the walls are not noticeably thickened, the only remaining explanation is that some change in the chemical or physical composition of the walls has taken place, in such a way that they have a greater affinity for the stain, anilin blue. In most of the diseased tissues the walls become brown. This color is probably due to the formation of tannins. There is always more or less of these substances in the walls, and when the cells begin to die, it is known that this browning often takes place through the work of the tannins. In several cases, also, granular deposits were found in various cells in the diseased regions only (of *Castanea*, *Pyrus*, etc.), similar to those described by ZIMMERMAN (**98**, § 207). Just what would cause this precipitation is not clear.

It was not always possible to determine which constituents of the host cell first showed the effect of fungous invasion. It is evident, however, that there is no general rule to be laid down. In *Smilacina*, for example, the chloroplasts seem to disappear before any of the other cell contents, while in *Pyrus* the nuclei of the sponge cells become enlarged before there are any other signs of change. It has already been pointed out that in some cases the cuticle and epidermis are affected first, as the fungus spreads from the center of infection, while in other cases no such result was observed.

The effects of the rust upon the leaf tissue are similar to those of gall-producing insects. The nuclei are enlarged, the protoplasm is often increased, and there is considerable hypertrophy. In other words, the rust seems to stimulate the tissue rather than to retard its growth. The witch brooms are evidences of such an influence, and MOLLIARD (**49**) describes such effects caused by insects in several hosts.

The effects of the fungous invasion upon the protoplast are various. At times the nuclei may entirely or almost entirely disappear from the diseased areas, leaving the cells, thus deprived of the nucleus, in a dead condition. This was noted in *Potentilla* and *Gaylussacia*. In other cases there is an unusual activity in the nuclear divisions, resulting in several nuclei in one cell. *Viola* and *Panicum* have already been cited as examples of this. The fact has already been given that the nuclei may also become larger than normal. The chromatin content of the diseased nuclei seems at times to become greater also. Such a condition is seen in *Panicum*, in which the nuclei of the diseased cells stain more intensely with hematoxylin than those of the normal cells. This may not be due to an actual increase in the chromatin, but either to a relative increase in the nuclear acid, or to a physical rearrangement of the chromatin. The chloroplasts may be reduced in size and finally disappear, as in *Potentilla*, or they may persist, as in *Viola*, until the final disintegration of the cell. The differences in the reactions of the cytoplasm and of the cell walls have already been cited in other connections.

With the attacks of parasitic fungi on leaves the effects are varied, depending upon the species of the host and of fungus. The virulence of the parasite and the degree of resistance of the host are the chief factors involved. If the leaf, while in actively growing condition, is attacked by the fungus, the changes in the host are often profound, if the fungus is able to maintain itself against the protective measures put in operation by the host. The cytologic changes already described are likely to occur. The leaf curl of peach caused by *Exoascus deformans* is an example of this type of change. Miss KNOWLES (**34**) has examined the leaf structure in this disease and has found that the tissue is greatly altered

by the presence of the fungus. The leaves are attacked in the bud and very soon after their emergence (DUGGAR 18). Cytologic changes may also occur when the fungus acts slowly for any reason. If the fungus is a weak parasite or if the host is not the best suited to the fungus, the host will have time to react to the fungus, and notable changes may be expected, both in the cell and in the tissue as a whole. That there is a difference in the speed with which various parasites work is seen from the fact that some diseased tissues show cells in various degrees of degeneration or death, while in others there is no intergrading condition between the dead, brown cells of the diseased area and the normal cells of the healthy tissue. The *Gaylussacia* described above shows relatively slow action of the parasite, as is proven by the two following conditions. First, the cells react by showing a granular protoplasm, then a uniform mass of broken-down protoplasm, which is stained brown, and finally nearly empty cell walls. It is improbable that this gradual degeneration is merely a process that would normally take place in cells which are breaking down, because often, as in *Castanea*, none of these intergrading forms are found. Second, it is to be noted that in *Gaylussacia*, and other hosts reacting similarly, the cuticle and the epidermal cells are often affected before the mesophyll, as the fungus spreads from the center of infection. This tends also to prove that the fungus acts progressively and slowly enough to be observed in the successive steps. *Psedera*, *Viola*, and *Panicum* act somewhat similarly in that they show changes in the size and number of nuclei, etc., as cytologic changes induced by the slow action of the respective parasitic fungi. It should be noted in passing, also, that in the case of the rust which was parasitized with *Darluca*, there was a different effect produced upon the nuclei of the leaf cells from that produced by the unparasitized rust. In the latter case the nuclei seem to have disappeared, while in the former case the nuclei are present but very abnormal (fig. 4). It is perhaps significant that nuclei were found only in places where the rust was parasitized, and presumably lowered in its vitality. If the latter statement is true, then the rust would not be able to act so quickly as normally, thus giving the host time to react to its influence.

In some of the diseases described, in which the tissue is killed and badly disorganized, few if any cytologic changes are to be noticed. The reason for this seems to be that the virulence of the fungus is relatively so great that the cells of the host are killed without having time to react to any stimulus. In such cases, as in the *Castanea*, all tissues seem equally affected, and there are no transition cells from the healthy to the dead portion. Another factor also which may operate is that the host tissue is old, and has not the power of reacting rapidly. This is in contrast with the young, highly resistant tissues, which, if parasitized, are able to react rapidly, and so present abnormal nuclear and other cytologic phenomena. *Smilax* also is an example of a diseased tissue which shows no cytologic changes.

A question constantly before the student of pathology is whether there is any way of judging the degree of susceptibility of a plant to disease. First of all it must be remembered that a plant may be easily attacked and injured by one disease-producing organism, and be quite immune to the attacks of another. Leaving this phase of the question, however, we ask, "Is the amount of hypertrophy a true indication of the degree of parasitism?" If we imply in the word "parasitism" some influence derogatory to the welfare of the plant, we are almost forced to answer the question in the negative, for in cases of symbiosis there is often great hypertrophy.

It is difficult at present to draw a sharp line between parasitism and symbiosis, since similar effects upon the host are noted in both. Thus, in some of the most noted instances of symbiosis, the mycorhizas, there is often considerable hypertrophy. Moreover, many kinds of galls do not seem to injure the host beyond the local tissue, and here again there is great hypertrophy. Hence, taken alone, an excessive enlarging of a portion of a plant is not sufficient evidence of the degree of parasitism. But, taken in conjunction with the cytologic changes induced in the host, hypertrophy becomes a valuable diagnostic feature. It must not be forgotten, however, that even in such cases the parasitic nature of the organism is not proved, for cytologic changes in mycorhizas have been reported, as noted heretofore. Evidence has previously been given in regard to the diagnostic value of the cytologic changes

in such tissues as the leaves of *Pyrus* and *Xanthium*. Here the hypertrophy is coincident with the changes in the constitution of the cell, and it indicates a rather strong parasitism. On the other hand, as in *Psedera* and *Gaylussacia*, the virulence is so great that the cytologic changes are simply the fleeting features of a rapid degeneration, and of course no hypertrophy could take place. Here again the condition indicates a strong parasitism. TUBEUF (**80**) points out that the degree of susceptibility of the host, or in other words the degree or strength of parasitism, is indicated by the amount and kind of deformation, as has just been indicated. He draws his illustration from the Uredineae. He says, "If the host suits the fungus only in a limited degree, then no hypertrophy will result, and the latter will attain only to the formation of spermagonia. Let the host, however, be the one best suited to the fungus, then hypertrophy will result and aecidia be developed." He gives as evidence a series of experiments upon *Gymnosporangium*, in which the fungus developed to different degrees varying with the host used. FENSTLING (**22**), in discussing the effects of rust upon their hosts, comes to the same conclusion regarding the relation of the degree of change to the time of the fungus attack.

In the leaf-inhabiting fungi, so far as studied, the mode of attack seems to be through the aid of some substance injurious or stimulative to the host cells. Two lines of evidence are at hand. The protoplasm of cells outside of the tissue directly in contact with the fungus often becomes killed, and the cell walls become brown. It is difficult to see how such a condition could exist if there is no toxic substance produced. In the second place, most of the cells of the host tissue examined by the writer contained no trace of the fungus, yet, as already shown, the nuclei are often enlarged or become numerous, and the chloroplasts also are reduced in size. Here again, there must be a substance which is diffusible through the cell walls, which is stimulative to the nucleus or poisonous to the chloroplasts. No indications were to be found as to the origin of such a substance. It is possible that the host cells may have produced it as a defensive measure, and that in turn certain of the cells were killed by this toxic substance. On the other hand, it is possible that the fungus may produce such a

poisonous substance which directly affects the host cells, as WARD (**86**) claims for the *Botrytis* fungus that causes the lily disease. WORONIN (**93***b*) attributes in an inferential way the effect of *Sclerotina Vaccinii* upon the cowberry to the same process. TUBEUF (**80**) quotes from him thus: "Here a peculiar phenomenon is exhibited, the fungus exerts its injurious effects on the *surrounding tissues* of the host plant, then, having killed these, it utilizes them as food material." Thus the tissues are killed first, apparently even beyond the immediate vicinity of the fungus, and are later used for food. That the parasitic fungi upon leaves produce this toxic substance is more easily believed than that the host produces it, and is itself killed by the protective measure. The nature of the poisonous substance, whether a chemical organic poison or an enzyme, could not be determined in the material at hand.

Another interesting question, whose answer may be at least partly suggested, has to do with the strict limitation of certain leaf-inhabiting fungi, such as the shot-hole fungi. This strict limiting of the area of influence of the fungus is shown in the *Smilax* disease described earlier in the paper. At the margin of the diseased area the leaf cells are killed and turned a deep brown to black. This discoloration may be due to the excessive production of tannins, and if so, this would probably explain why the fungus proceeds no farther. BOKORNY (**5***b*) has found that tannins will inhibit the growth of fungi, and it seems quite likely that the production of tannins in the leaf finally stops the further growth of the fungus.

Summary

In the review of the previous work, it was found that many changes have been noticed in the organs and tissues of flowering plants. The cytologic changes, however, were especially emphasized. Very little work has previously been reported upon the effect of fungi on the cell contents of leaves, and the writer has shown that in such cells the nuclear and protoplasmic changes, which other workers have noted in cells of other plant organs attacked by parasites or under the influence of other destructive agents, also occur in leaf tissues when attacked by the parasitic fungi examined.

I wish here to thank Dr. T. J. BURRILL of the University of Illinois, under whom these investigations were carried on, for the privileges of the department extended to me, and Dr. CHARLES F. HOTTES of the same department, and Dr. H. A. GLEASON of the University of Michigan, for their kindly criticism of portions of the manuscript.

UNIVERSITY OF TENNESSEE
KNOXVILLE, TENN.

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THE INFLUENCE OF THE SEED UPON THE SIZE OF THE FRUIT IN STAPHYLEA. II

J. Arthur Harris

(with one figure)

IV. On the nature of the correlation between the number of seeds and pod length

Heretofore we have contented ourselves with such analysis of our data as is necessary to the establishment on a sound quantitative basis of the fact of a correlation between the number of seeds developing and the length of the pod. This correlation is that of the statistician, not of the physiologist. It shows the existence of a relationship between two characters and measures its intensity. It does not prove that this relationship is due to a direct physiological interdependence between the two characters. To demonstrate such physiological interdependence one must remove the influence of other possible factors. All of the factors which seem possible sources of the correlation between the number of seeds developing and pod length and which can be investigated on the available data are discussed below.

1. THE HYPOTHESIS OF THE INFLUENCE OF THE RELATIONSHIP FOR OVULES AND LENGTH

As emphasized in the paper on *Cercis*, one of the sources of confusion in interpreting an observed r_{ls} is the fact that both l and s may be correlated with o, and so differences in the fruit length (l) which appear to be due directly to the number of seeds developing may be merely resultants of the relationship r_{lo} and r_{os}, and so indicate no physiological relationship between s and l. But it has been conclusively shown that $r_{ls} > r_{lo}$, thus demonstrating that the interdependence for seeds and length is not solely dependent upon the relationship for ovules and length. Indeed, it is only when both r_{lo} and r_{os} are high that they will greatly affect r_{ls}. It seems desirable, however, not to leave the question without showing just how much influence may be attributed to this factor. I use the two methods suggested in the paper on *Cercis*, namely, the corre-

lation for length and seed/ovule index and the partial correlation coefficient. Comparing r_{ls} and r_{li} for the combined series we have:

Relationship	1906—2050 pods	1907—1218 pods
Number of seeds and length, r_{ls}....	0.3522±0.0131	0.2019±0.0185
Seed/ovule index and length, r_{li}....	0.3418±0.0132	0.2018±0.0185
Difference, $r_{ls}-r_{li}$.....	0.0104±0.0186	0.0001±0.0261

Both differences are less than their probable errors, and of no significance.[1]

Consider now the correlation between s and l for constant values of o, as measured by the partial correlation coefficient of ρ_{ls}. The correlations for number of ovules formed and number of seeds developing per locule (r_{os}) are necessary. The tables of data are 36 in number, and since they are supplementary rather than fundamental to our main subject, we need not publish them. The constants with their probable errors are set forth in tables XI and XII.

TABLE XI

Number of shrub	r_{os} Correlation, ovules and seeds	r/Er
11.....	−0.076±0.037	2.06
12.....	0.042±0.035	1.19
13.....	0.154±0.037	4.16
14.....	0.112±0.038	2.96
15.....	−0.131±0.037	3.54
16.....	−0.063±0.039	1.61
17.....	0.080±0.039	2.05
18.....	0.002±0.039	0.05
19.....	−0.038±0.039	0.96
20.....	0.045±0.037	1.20
21.....	−0.094±0.039	2.40
22.....	0.028±0.039	0.71
23.....	0.014±0.039	0.36
24.....	0.144±0.038	3.78
25.....	0.078±0.039	2.00
26.....	0.026±0.039	0.67
27.....	0.048±0.039	1.22
28.....	0.093±0.038	2.45
29.....	0.058±0.039	1.48
30.....	0.042±0.039	1.08

TABLE XII

Number of shrub	r_{os} Correlation, ovules and seeds	r/Er
11.....	0.156±0.060	2.60
17.....	0.021±0.054	0.39
19.....	−0.072±0.046	1.56
24.....	0.159±0.038	4.23
29.....	0.028±0.047	0.60
31.....	0.057±0.038	1.50
32.....	0.094±0.043	2.18
33.....	0.126±0.126	3.19
34.....	0.025±0.025	0.56
35.....	0.079±0.079	1.73
36.....	0.150±0.049	3.08
37.....	0.004±0.040	0.10
38.....	0.033±0.040	0.82
39.....	0.137±0.059	2.33
40.....	0.045±0.039	1.16
41.....	0.010±0.050	0.19

[1] Possibly we are not quite justified in using the ordinary method of calculating the probable error of a difference here, that is, the square root of the sum of the squares of the two probable errors, but the differences in the correlation are so very small that it makes no practical difference.

In 1906, 15 of the constants have the positive and 5 the negative sign; in 1907, only one of the 16 is negative. Throughout, the values are too low to be of any practical significance. The mean for 1906 is 0.0282, and for 1907 it is 0.0658. We have already found low values for r_{lo}, and with the very small values for r_{so} just demonstrated, it seems hardly worth while to calculate ρ_{ls}. But, using the formula $\rho_{ls}=\frac{r_{ls}-r_{lo}r_{so}}{\sqrt{1-r_{lo}^2}\sqrt{1-r_{so}^2}}$, and substituting the mean values of the constants for the individuals as the most trustworthy measures for the physiologist, we find:

Relationship	1906—20 shrubs	1907—16 shrubs
Average r_{lo}	0.1282	0.1240
Average r_{so}	0.0282	0.0658
Average r_{ls}	0.3868	0.3636
Calculated ρ_{ls}	0.3865	0.3591
$r_{ls}-\rho_{ls}$	0.0003	0.0045

Obviously there is no practical significance whatever to be attached to the differences such as 0.0003 and 0.0045. In *Cercis*, r_{ls} is very materially reduced when allowance is made for the influence of the number of ovules. The two foregoing methods show that in *Staphylea* r_{ls} is essentially independent of r_{lo} and r_{so}.

2. THE HYPOTHESIS OF MECHANICAL STRETCHING

Where the seeds in a locule attain a considerable size and are numerous, it is quite possible that an increased size of the fruit might result from their space requirements, through the purely mechanical effects of crowding. In *Cercis* the seeds are relatively small and, generally at least, not in contact. Mechanical stretching seemed almost entirely excluded by the nature of the material, and I gave no attention to it. In *Staphylea* there seems even less reason to suppose this factor to be of any importance, but it is well to have such conclusions based on actual statistics. To test whether there is a sensible influence of the spatial requirements of the seeds upon the length of the pods, I think we may proceed as follows.

Clearly there can be little mechanical stretching of the placental space due to the development of a single seed in a locule. All the

room which it demands is that necessary for its attachment; the pressure of adjoining seeds is a factor entirely removed. *Staphylea* has the advantage that the number of seeds developing is so small that it is easy to select material in which the stretching of the pod by a crowding of the seeds can hardly be a possibility. For pods with one to three seeds, there may be only a single seed in each

TABLE XIII

Class	1906		1907	
	f	Mean length	f	Mean length
1 Seed				
1–0–0	960	5.57	519	6.26
2 Seeds				
1–1–0	291	6.39	227	6.83
2–0–0	204	6.46	105	6.96
3 Seeds				
1–1–1	57	7.23	32	7.19
2–1–0	172	6.97	117	7.21
3–0–0	47	7.21	26	6.96
4 Seeds				
2–1–1	64	7.56	40	7.38
2–2–0	33	7.39	15	7.33
3–1–0	39	7.90	23	7.61
4–0–0	14	7.64	5	7.80

locule, that is, seed formulae: 1–0–0, 1–1–0, 1–1–1. When more than three are produced, one of the locules must have two or more. Now the problem is simply this; given fruits producing the same number of seeds, are those in which two or more of the seeds are produced in the same locule larger than those in which but a single seed is produced in each locule?

Table XIII gives the number of pods available and the mean length of pod for the chief seed-formulae (including about 91 per cent of the whole number of fruits available) for the 1906 and 1907 series. The results are also shown graphically in fig. 5. Here the solid dots give the empirical means for the individual seed-formulae for 1906 and the circles those for 1907. The vertical lines (solid for 1906 and broken for 1907) indicate the mean length of pods with 1, 2, 3, and 4 seeds per pod, irrespective of the distribution of these seeds among the locules. Certainly there is no clear evidence in this figure that pods in which the seeds are grouped in less than

three locules are longer than those in which they are as much distributed as possible among the three. It follows that mechanical

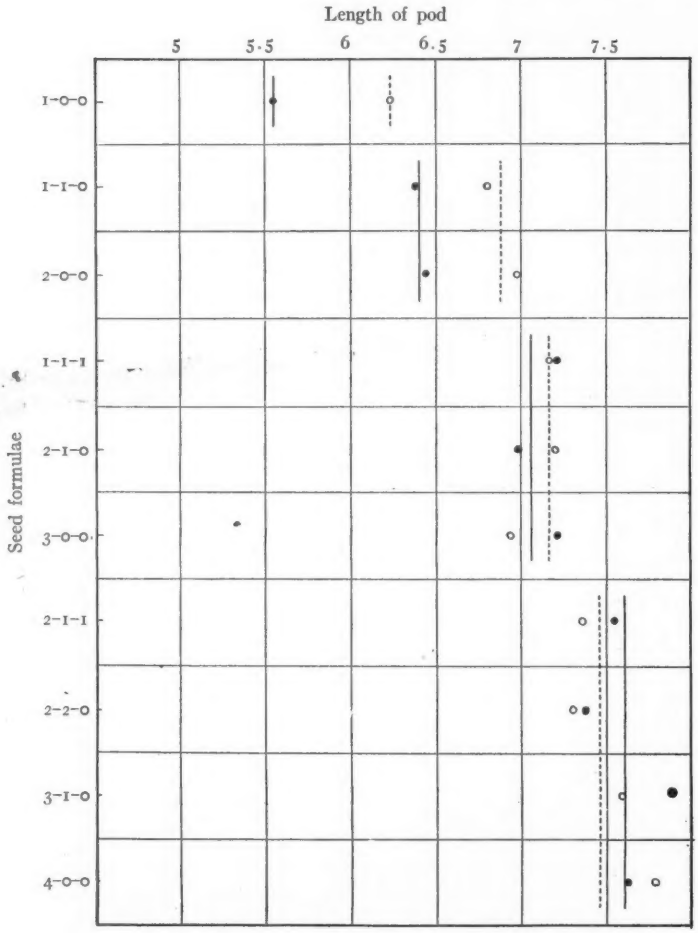

FIG. 5.—Mean lengths of pod for different seed-formulae and total number of seeds per fruit; solid dots and lines = 1906; circles and broken line = 1907.

stretching of the pod has had little or no part in the bringing about of the correlation between length and number of seeds developing.

3. THE HYPOTHESIS OF THE MUTUAL DEPENDENCE OF FRUIT LENGTH AND FERTILITY UPON OTHER CHARACTERS OF THE PLANT

Two characters both positively or negatively correlated with a third are correlated with each other. This is doubtless the source of much of the correlation found between organs. Possibly r_{lo} and r_{ls} indicate no physiological interdependence between l and o or l and s, but are due merely to l, o, and s being influenced by the position of the fruit on the inflorescence or by the number of pods per inflorescence. The correlation between the length of the pod and the distance of the flower-bearing node at which it is produced from the base of the inflorescence[2] is shown for the 1906 series[3] in table XIV, 1906, and for number of pods developing per inflorescence and length of pod in table XV, 1906. These give:

$$\text{Position and length, } r_{pl} = -0.0580 \pm 0.0148$$
$$\text{Number and length, } r_{nl} = -0.1828 \pm 0.0144$$

Statistically these values are certainly trustworthy, for $r_{pl}/E_r = 3.91$, and $r_{nl}/E_r = 12.70$. They indicate that both a more distal position on the inflorescence and a number of fruits above the normal is prejudicial to the maximum development of the fruit.[4]

If it be found that the number of seeds developing is also negatively correlated with the position and with the number of the

TABLE XIV, 1906

LENGTH OF FRUIT

Position	3	4	5	6	7	8	9	10	11	Totals
1.....	1	65	192	322	259	125	62	20	1	1047
2.....	4	50	167	197	143	88	31	9	..	689
3.....	1	25	69	75	54	31	14	2	..	271
4.....	..	2	9	13	6	4	5	1	..	40
5.....	..	..	...	3	...	...	...	..	..	3
Totals	6	142	437	610	462	248	112	32	1	2050

[2] The serial position of the node on the inflorescence counting from the base.

[3] Data for position are not available for 1907. Because of a severe frost many of the inflorescences produced only a single fruit, and it seems idle to study the number per inflorescence.

[4] Inflorescences with larger numbers of fruits will have more distally placed fruits. I have not worked out the correlation between these two characters, but if it is considerable the two constants just discussed are not independent, and probably one or both should be, biologically considered, more nearly o.

TABLE XV, 1906

LENGTH OF FRUIT

Fruits in infl.	3	4	5	6	7	8	9	10	11	Totals
1.....	..	..	..	..	1	..	..	..	..	1
2.....	..	8	36	44	59	40	26	8	1	222
3.....	1	22	85	167	127	66	41	8	..	517
4.....	2	38	120	166	112	73	28	10	..	549
5.....	1	40	90	115	88	42	7	2	..	385
6.....	1	31	65	61	34	14	6	3	..	215
7.....	..	2	20	20	21	7	4	1	..	75
8.....	1	1	13	28	10	3	..	..	..	56
9.....	..	..	2	2	4	1	..	..	..	9
10.....	..	..	3	3	2	1	..	..	..	9
11.....	..	..	..	..	..	..	..	..	..	..
12.....	..	..	3	4	4	1	..	..	..	12
Totals	6	142	437	610	462	248	112	32	1	2050

fruits developing on an inflorescence, we should expect a positive correlation between number of seeds developing and length of pod, due to no direct physiological interdependence of the two, but solely to their correlation with these other characters. Turning to our data, we see the correlation surface for position and seeds per locule in table XVI, 1906, and between number per inflorescence and seeds per locule in table XVII, 1906. To the eye there seems to be little or no correlation. The calculating machine shows:

For position of fruit and seeds, $r_{ps} = -0.0148 \pm 0.0149$
For number of fruits and seeds, $r_{ns} = -0.0474 \pm 0.0148$

Again the signs are negative, but the values are so low that little importance can be safely attached to them.

With such low correlations, it seems hardly worth while to consider the amount of influence which position on the inflorescence or number of pods per inflorescence would have upon the degree of interdependence of s and l, but since biometricians are frequently criticized for neglecting just such biological considerations as this, I calculated the correlation for seeds and length for constant numbers of pods per inflorescence. Number rather than position was chosen, since the correlations are numerically higher and will have greater influence on r_{sl}. Working from the formula

$$\rho_{sl} = \frac{r_{sl} - r_{ns} \cdot r_{nl}}{\sqrt{1 - r_{ns}^2}\ \sqrt{1 - r_{nl}^2}},$$

we find:

$$r_{sl} = 0.3522 \pm 0.0131,$$
$$\rho_{sl} = 0.3498 \pm 0.0131,$$

$$r_{sl} - \rho_{sl} = 0.0024 \pm 0.0185$$

TABLE XVI, 1906

SEEDS PER LOCULE

Position	0	1	2	3	4	5	6	Totals
1.....	1533	1109	355	115	33	11	..	3156
2.....	1076	733	190	60	16	4	..	2079
3.....	404	285	88	28	7	1	..	813
4.....	56	40	12	9	2	..	1	120
5.....	5	3	1	....	..	..	..	9
Totals.....	3074	2170	646	212	58	16	1	6177

TABLE XVII, 1906

SEEDS PER LOCULE

Fruits per infl.	0	1	2	3	4	5	6	Totals
1.....	2	....	1	....	..	..	..	3
2.....	299	238	82	29	14	4	..	666
3.....	761	556	170	54	15	4	..	1560
4.....	827	581	164	60	16	5	..	1653
5.....	591	399	120	37	7	1	..	1155
6.....	343	217	63	17	5	2	1	648
7.....	115	85	25	6	..	..	..	231
8.....	91	61	13	2	1	..	..	168
9.....	10	14	2	1	..	..	..	27
10.....	14	10	2	4	..	..	..	30
11.....	....	....	....	....	..	..	..	....
12.....	21	9	4	2	..	..	..	36
Totals.....	3074	2170	646	212	58	16	1	6177

The reduction in correlation is only about one-eighth of the probable error of the determination! Further arithmetic or discussion would be pedantic. I conclude that the correlation between the number of seeds developing and the length of the fruit is not merely a secondary result of the correlation of these two characters with position on the inflorescence or number of pods per inflorescence, but must be due to some force operating in the developing fruit itself.

For *Cercis* I have no data for the relationship between the number of pods per inflorescence and the fertility and length characters

of the fruits, but it may be of some interest to determine the correlation between the number of ovaries and the number of ovules per ovary for the three series of intact inflorescences gathered in the spring of 1907.[5] The data for r_{no} are given in tables XVIII and XIX.[6] The coefficients of correlation[7] are

$$\text{Tree 1, } r = -0.007 \pm 0.023$$
$$\text{Tree 2, } r = 0.030 \pm 0.021$$
$$\text{Tree 3, } r = 0.134 \pm 0.024$$

In the first two cases the correlations are certainly insignificant. In the third tree there is a slight correlation which is about six times its probable error. Ordinarily this would be considered trustworthy, but the actual number of ovaries instead of the

TABLE XVIII, CERCIS

Ovaries per inflorescence	Tree 1		Tree 2		Tree 3	
	Number of ovaries	Total ovules	Number of ovaries	Total ovules	Number of ovaries	Total ovules
5	...	...	5	27	25	125
6	6	44	...	...	112	532
7	84	647	...	...	139	672
8	197	1515	15	76	214	1043
9	176	1344	26	146	181	895
10	209	1585	130	679	49	243
11	142	1095	283	1495	11	60
12	47	359	297	1596	...	...
13	...	...	168	897	...	...
14	27	207	139	763	14	75
15	...	...	15	89	...	...
16	...	...	...	...	...	...
17	...	...	...	...	17	92
Totals	888	6796	1078	5768	762	3737

[5] Harris, J. Arthur, Is there a selective elimination of ovaries in the fruiting of the Leguminosae? Amer. Nat. **43**:556–559. 1909.

[6] Again the different inflorescence grades are necessarily weighted with the number of flowers which they bear, and the means and standard deviations used in determining the coefficients of correlation are calculated from these weighted frequencies. Sheppard's correction was not used. The single case of no ovules is probably due to one of the ovaries being still too young. In dissecting the ovaries out of the flowers, clearing, and examining under the lens, some accidents are unavoidable. There is no reason to believe that the 35 ovaries which were broken or ruined in clearing differed from those which could be counted. They are simply omitted in the calculations.

[7] Calculated by method described in Amer. Nat. **44**:693–699. 1910.

TABLE XIX, CERCIS

NUMBER OF OVULES PER OVARY

	0	1	2	3	4	5	6	7	8	9	10
Tree 1.....	..	..	..	..	3	1	49	279	476	76	4
Tree 2.....	1	1	5	32	177	327	431	100	4	..	..
Tree 3.....	..	..	10	23	198	341	179	11	..	..	..

number of inflorescences was used in calculating the probable error. This is perhaps justifiable, but had N been taken as 100, the actual number of inflorescences, the probable error would have been much higher, and in the third tree the correlation would have been only about twice or thrice its probable error. On the basis of available data, there is no demonstrable relationship, therefore, between the number of ovaries on an inflorescence and their characteristics.

4. THE HYPOTHESIS OF THE INDIVIDUALITY OF INFLORESCENCES

It has now been shown that neither position nor number of pods has sufficient relationship with the two characters immediately under consideration to produce a sensible correlation between them. Theoretically both p and n would influence, to some extent, the quantity of plastic material available for a given fruit, but so far as these evidences go, similarity of nutrition for both seeds and fruit wall has little influence in bringing about the correlation between them. These are not the only factors which might influence the food supply of a developing fruit. Some inflorescences may be much more generously supplied with fruit and seed building substances than others, and in the distribution of this material throughout the inflorescence, position of pod may have a negligible significance, and number of pods developing be of only small importance.

I believe the following method to be satisfactory in determining whether r_{ls} is due to the differentiation between the inflorescences of an individual either (*a*) in the capacity for development of the protoplasm of which their ovaries are made up, or (*b*) in the availability of food material for the expansion of these organs.

If both the pod length and the number of seeds developing are influenced by the nature of the inflorescence upon which they are

borne, or by the quantity of the plastic material which it receives from the shrub, in a way to bring about a correlation between the length of a pod and the seeds which it matures when the pods from an individual are used as a sample, there should be a correlation between the number of seeds developing in a fruit and the length of another fruit on the same inflorescence. In short, if there is something inherent in the inflorescence which tends to influence both number of seeds developing and length of fruit in the same sense, so that a correlation arises between them, this influence should effect in some degree all pods with the result that the cross correlation between number of seeds developing in one pod and length of another pod should have a sensible positive value.

The only disadvantage of this method is its extreme laboriousness. It is necessary to draw up tables between the characters of the fruits of the same inflorescence, just as in a study of heredity one prepares tables showing the correlation between brothers in the same family. Each pod is used once in association with every other pod on the same inflorescence. The number of combinations thus secured will be $\frac{1}{2}n(n-1)$, and since for practical purposes we use each fruit once as a first and once as a second member of an associated pair,[8] we have for each inflorescence $n(n-1)$ combinations.

All inflorescences have not the same number of pods, and an inflorescence with six locules will give relatively fewer entries in the symmetrical table than one with twelve. I regret the necessity of thus giving weight to the larger inflorescences, but since the

[8] For the intra-inflorescence relationship for the length of the fruit it is only necessary to draw up tables showing all possible combinations of the fruit lengths of the same inflorescence. But for ovules and seeds we are dealing with the individual locules, and there are three to each fruit. If we made every possible combination in the preparation of the tables, we would be correlating, in some cases, between the locules of the same fruit, and, in some cases, between the locules of different fruits on the same inflorescence. The point which we wish to get at is the relationship between the different fruits of the same inflorescence. The plan followed, therefore, has been to correlate the number of ovules formed or the number of seeds developing in each locule with the number in every other locule on the inflorescence, except those of the same fruit. In the same manner, in dealing with the relationships between length of pod and the fertility characters, the tables were so drawn as to show the relationship between the length of the pod and the fertility characters of all the locules on the inflorescence, except its own three.

correlations between the number of pods per inflorescence and all the characters of the pod are generally very low, it hardly seems worth the labor to reduce all the inflorescences to a standard frequency to avoid weighting. Designating the two characters of a pair which are being compared as "first" and "second," and indicating them by one and two dashes respectively, we have the following relationships for consideration.

Ovules of first locule and ovules of second locule, $r_{o'o''}$
Seeds of first locule and seeds of second locule, $r_{s's''}$
Length of first pod and length of second pod, $r_{l'l''}$
Length of first pod and ovules per locule in second pod, $r_{l'o''}$
Length of first pod and seeds per locule in second pod, $r_{l's''}$

Since the pods from each shrub must be treated separately, this requires the preparation of 100 correlation tables, containing some hundreds or thousands of entries each. These have been carefully prepared and verified, and the means and standard deviations used in obtaining the correlation coefficients calculated anew for all the characters from the weighted frequencies. The tables and constants are too bulky for publication. The end results

TABLE XX

INTRA-INFLORESCENCE CORRELATION COEFFICIENTS

Shrub	Ovules of first locule and ovules of second locule	Seeds of first locule and seeds of second locule	Length of first pod and length of second pod	Length of first pod and ovules per locule in second pod	Length of first pod and seeds per locule in second pod
11	0.516	0.098	0.517	−0.387	0.190
12	0.037	0.004	−0.003	−0.217	−0.091
13	0.078	−0.025	0.009	0.051	−0.008
14	0.093	−0.017	0.017	0.027	0.008
15	0.113	0.034	0.178	0.049	0.046
16	0.088	−0.009	0.113	0.083	−0.030
17	0.108	0.017	0.244	0.317	0.008
18	−0.026	−0.028	−0.045	0.020	−0.087
19	0.084	−0.017	−0.036	−0.068	−0.020
20	0.123	0.031	0.109	0.074	0.049
21	0.143	0.003	0.052	−0.067	0.000
22	0.026	0.020	0.059	0.007	0.039
23	0.084	0.015	0.018	−0.031	−0.014
24	0.093	−0.034	−0.007	0.010	−0.052
25	0.515	0.096	0.378	0.206	0.183
26	0.099	0.042	0.115	0.044	0.062
27	0.059	−0.038	0.058	0.117	−0.038
28	0.330	0.009	0.151	−0.029	−0.020
29	0.054	−0.009	0.197	0.044	0.034
30	0.185	0.003	0.124	0.026	−0.011

TABLE XXI

SUMMARY OF INTRA-INFLORESCENCE CORRELATION COEFFICIENTS

	OVULES AND OVULES		SEEDS AND SEEDS		LENGTH AND LENGTH		LENGTH AND OVULES		LENGTH AND SEEDS	
	f	Average	f	Average	f	Average	f	Average	f	Average
Positive...	19	+0.149	12	+0.031	16	+0.146	14	+0.077	10	+0.062
Negative..	1	−0.026	8	−0.022	4	−0.023	6	−0.133	10	−0.037
Total...	20	+0.140	20	+0.010	20	+0.112	20	+0.014	20	+0.025

appear in table XX, and these are still further summarized in table XXI.

The intra-inflorescence correlation for ovules is unquestionably positive, and perhaps high enough that one safely can say that the inflorescences are differentiated among themselves with respect to number of ovules produced. For number of seeds per locule the inflorescences seem not at all differentiated; it is not even possible to ascertain the sign of $r_{s's''}$, and its mean is only 0.010. This result seems to me of considerable physiological interest. I had expected to find a greater similarity among the numbers of seeds developing in the locules of the inflorescence than among the numbers of ovules formed. I thought that probably some inflorescences would be in much more advantageous positions for obtaining food material than others, and that in consequence the differences between inflorescences would be greater (and consequently the intra-inflorescence correlation higher) than for number of ovules. So far as we can judge from evidence at hand, the morphogenetic factor is stronger than the physiological[9] in determining the characteristics of the fruits of an inflorescence. For length, it seems reasonably certain that there is a slight similarity between the pods

[9] One must use extreme caution in such fields as this, for there are innumerable pitfalls. By morphogenetic I mean the organogenetic processes which give rise to the ovaries. By physiological factors I refer to (*a*) the ecological factors which determine whether an ovule shall receive a sperm, (*b*) to the availability of food material and other requisites for growth, (*c*) the innate vigor of the individual inflorescences which determine whether a fertilized ovule shall develop into a seed. The third of these is probably in some measure identical with the organogenetic. If (*a*) and (*b*) were really very different for the several inflorescences of an individual, one would expect the intra-inflorescence correlation for number of seeds to have sensible values and possibly to rise considerably above what it is for ovules. This is the case in *Sanguinaria* (Biometrika **7**:328. 1910), where it seems that the main bulk of the

of the same inflorescence as compared with those of the tree in general.

Finally, the results from the two correlations fundamental to our present purposes are unmistakable. The evenness of the division between positive and negative and the extremely low mean value of the coefficients $r_{1'0''}=0.014$ and $r_{1'1''}=0.025$ prove that there is no material relationship between the length of one pod and the number of ovules or seeds in another pod of the same inflorescence. This seems to me to prove conclusively that there are no differences in the supply of plastic materials of the different inflorescences sufficient to account for both the number of seeds developing and the length of an individual fruit deviating from their means in the same way.

For *Cercis* I have no data for the mature inflorescence comparable with that for *Staphylea*. It is interesting, however, to compare the intra-inflorescence correlations for number of ovules in the ovaries collected at flowering time in the spring of 1907 with the results obtained for *Staphylea*. The data for $r_{0'0''}$ are given in table XXII.[10] The correlations are

Tree 1, $r=0.571\pm0.015$
Tree 2, $r=0.213\pm0.020$
Tree 3, $r=0.378\pm0.021$

Mean, $r=0.388$

These results indicate a differentiation among the inflorescences of an individual of *Cercis* somewhat higher than we have found in *Staphylea*, but three individuals are not sufficient for more than a suggestion. The finding of an intra-inflorescence correlation in another genus gives confidence in the results for *Staphylea*. Should

correlation between the placentae of the fruit is due to ecological and physiological factors. There, however, we were dealing with individuals subjected to an external environment, not with the several inflorescences of the same individual. Possibly (*a*) and (*b*) are optimum for all inflorescences, but only a small percentage of the seeds develop because of some internal limiting factor. The bladdery fruits are possibly adaptive, and too great a weight of seed would offset the advantage of the peculiar structural features.

[10] Calculations by method described in Amer. Nat., 1910, The "ovules of first ovary" gives the grade, and the "number of associated ovaries" gives the frequencies for both variables, the tables being symmetrical.

TABLE XXII, CERCIS

Ovules of first ovary	Tree 1		Tree 2		Tree 3	
	Number of associated ovaries	Total ovules in associated ovaries	Number of associated ovaries	Total ovules in associated ovaries	Number of associated ovaries	Total ovules in associated ovaries
0	....	....	11	56	....	....
1	....	....	11	61	....	....
2	....	....	55	294	65	319
3	....	....	348	1891	168	854
4	21	163	1874	10096	1346	6594
5	7	55	3466	18422	2309	11330
6	409	3142	4600	24593	1358	6806
7	2322	17696	1118	6130	98	494
8	3984	30520	53	298	....	....
9	626	4813	....	....	....	....
10	27	214	....	....	....	....
Totals	7396	56603	11536	61841	5344	26397

an intra-inflorescence correlation for number of seeds and for length of pod be sometime demonstrated for matured fruits of *Cercis*, it would indicate that in this species a somewhat lower proportion of r_{ls} is due to a direct physiological relationship between the two characters than is indicated by the constants already calculated.

5. THE HYPOTHESIS OF THE DIFFERENTIATION OF INDIVIDUALS

If a sample of pods be made up of collections from a series of individuals, a (statistical) correlation will be found between two characters of the pod, say length and number of seeds, whether there is any physiological relationship or not, providing that the individuals are differentiated among themselves with respect to both of the characters in such a way that in the several individuals of the series both characters of the pair tend to fall above or below the means for all the individuals. Concretely, we understand for our present material that if, because of innate vigor or by reason of favorable environment, some individuals bore both larger pods and more seeds than the average, while other individuals with less innate vigor or with less favorable environment produced both smaller pods and fewer seeds than the average, then the correlation table prepared for the whole series of pods would show a sensible

interdependence for length and seeds which would not be due to any direct physiological relationship at all, but solely to differentiation in the plants which produced them.

The criticism that the correlations for pod characters may be due to heterogeneity of material has already been met for the present study, by analyzing the data from each individual independently. To make assurance doubly sure, we may determine the correlations (*a*) between the mean length of the fruit and the mean number of ovules per locule (r_{lo}), and (*b*) between the mean length of the fruit and the mean number of seeds per locule (r_{ls}), for the individual trees. Working by the brute force method we get

1906	1907
$r_{lo}=0.004\pm0.150$	0.010 ± 0.168
$r_{ls}=0.418\pm0.124$	-0.371 ± 0.145

In both years r_{lo} is only a fraction of its probable error, and no significance whatever can be given it. Statistically, r_{ls} may be significant in both cases; for in 1906 $r/E_r=3.36$, and in 1907 $r/E_r=2.55$. Biologically the two constants, of roughly the same numerical order but opposite in sign, mean nothing except that mean length and mean seeds do not seem to be closely related. Probably both are determined by largely independent causes. The substantial quantitative results are due solely to the probable errors of sampling.[11]

[11] Reconsider in the light of these results the peculiar condition noted in table V, where it appeared that both r_{lo} and r_{ls} are lower for the population than for the mean values of these constants for the samples from individual trees. The explanation seems to be quite simple. The magnitude of r depends upon the largeness of the denominator, $\sigma_l\sigma_o$ or $\sigma_l\sigma_s$, as well as upon the numerator, S(lo) or S(ls), of the correlation formula. The mean $\sigma_{ls}\sigma_{os}\sigma_s$ of the individuals are seen in table V to be much lower than the same constants for the population. For both series the correlation between A_l and A_o is insignificant, and consequently we see a low value for r_{lo} for the population because of the high value of $\sigma_l\sigma_o$. This is also the tendency for r_{ls}, but in this case, the inter-individual correlation for A_l and A_s have material values which, although without biological significance because of their high probable errors, nevertheless have their influence upon the correlation constants for the population. In 1906, the inter-individual correlation is positive, and this tends to raise the population constant to about the same value as that for the mean of individuals, that is, 0.352 as compared with 0.387; but for 1907, the inter-individual correlation for means is negative and we find the discrepancy of 0.202 against 0.364. These results emphasize the importance of a stringently analytical treatment of data.

6. OTHER HYPOTHESES

The foregoing hypotheses have seemed the most reasonable ones to explain the relationship between the length of the fruit and the number of seeds developing, without the assumption of a direct causal relationship between them. All have given negative results in the sense that they have failed to show any reason for the interrelationship between length and number of seeds external to the two characters themselves. This does not prove that there is a direct causal relationship between them, that is, that their interdependence is not due to some outside influence, but I think that the factors suggested are the most important ones, and I have no data for taking up others on the present material.

We may conclude, therefore, with reasonable confidence, that the developing seed does in some way exert a developmental stimulus on the ovary wall. The nature of this stimulus must be ascertained by further studies.

V. Recapitulation

The chief problems, methods of reasoning, and conclusions from observations detailed both above and in an earlier paper on *Cercis*, may be briefly reviewed here.

That pollination is in many cases a stimulus to the development of the ovary now seems fairly well established. Several biologists have suggested that the developing seed also exerts an influence upon the growth of the fruit.

The establishment of this second hypothesis presents far greater difficulties than that of the first. So far as I am aware, no one has isolated bodies from the growing seed which when introduced into other ovaries accelerates development. Nor has it been proved that young ovaries with larger numbers of developing seeds show a higher rate of growth; and even if this were demonstrated, it would be impossible to say that the acceleration of growth was not due to the stimulation of an unusually large number of pollen tubes.

The most feasible method for a preliminary study seems to be to work with mature fruits and to ascertain whether the number of seeds may have had an influence in determining the size of the

fruit. If the size of the fruit increases as the number of seeds becomes larger, the development of the seed must exert a stimulus to the development of the fruit wall, providing that the correlation between the number of seeds and the size of the fruit is not due to some other factor or factors upon which both seed number and fruit size are in some degree dependent.

The task is, therefore, twofold: (*a*) to obtain a measure of the correlation between the number of seeds and the length of the fruit, and (*b*) to show by a process of elimination that the correlation can, with a high degree of probability, be attributed to a direct physiological relationship between number of seeds and size of fruit.

I. The first of these undertakings is straightforward. The coefficients of correlation show that in both *Cercis* and *Staphylea* there is a very substantial interdependence between number of seeds and fruit length.

II. The second task is somewhat more complicated. The following facts indicate that this observed interdependence is due to physiological factors confined to the seed and ovary wall:

(1) In *Staphylea* the correlation between the total number of seeds and the length of the fruit is higher than that between the number per locule and length.

(2) The relationship between the number of seeds developing and the length of the pod is in large measure independent of the influence of the number of ovules.

(3) In both *Cercis* and *Staphylea* the possibility of a mechanical stretching of the fruit through the pressure of adjoining seeds seems to be excluded.

(4) Both length of pod and number of seeds developing are slightly correlated with the number of fruits per inflorescence and with the distance of the node from the base of the inflorescence, but the correlations are too low to be of any significance in producing the relationship between the number of seeds and length of pod.

(5) The inflorescences of a shrub of *Staphylea* seem to be slightly differentiated with respect to the number of ovules per locule and the length attained by the fruit. Apparently the inflorescences

are not at all individual in the number of seeds developing per locule in the fruits which they produce. The cross correlation coefficients for the number of seeds in one fruit and the length of another fruit of an inflorescence furnishes no indication that there are innate or environmental peculiarities of inflorescences which tend to influence both the number of seeds developing and the length of the fruit in the same direction. In short, one cannot explain the correlation between number of seeds and length as the result of superior innate vigor or favorable nutrition in some inflorescences of an individual and the contrary conditions in others.

III. From the immediately foregoing considerations, and from others detailed in the body of the paper, we seem to be justified in the conclusion that the measurable interdependence between the number of seeds and the length of the fruit in *Staphylea* and probably also in *Cercis* is a direct physiological one, and that the two characters stand in some degree in the relationship to each other of cause and effect.

While this conclusion has already been reached by some other biologists depending upon more general evidence, I believe that this and the preceding study are the first in which a fairly satisfactory approximation to proof has been attained. A chief value of these studies is that the numerous difficulties surrounding the problem have been more clearly realized than appears to have been done before. The numerical results, while substantiating in a satisfactory manner the conclusions drawn from them, must be looked upon as merely approximations.

CARNEGIE STATION FOR EXPERIMENTAL EVOLUTION
COLD SPRING HARBOR, N.Y.

THE VEGETATION OF SKOKIE MARSH, WITH SPECIAL REFERENCE TO SUBTERRANEAN ORGANS AND THEIR INTERRELATIONSHIPS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 155

EARL E. SHERFF

(WITH TEN FIGURES)

The work on which this paper is based was begun in the autumn of 1910 and was concluded in the autumn of 1911. The detailed study of subterranean organs was carried on chiefly in the summer of 1911. The writer gratefully acknowledges his indebtedness for many valuable suggestions and much helpful advice, to Dr. HENRY C. COWLES and to Mr. GEORGE D. FULLER, under whose joint supervision the investigation was pursued, and also to Dr. J. M. GREENMAN for certain taxonomic assistance.

Skokie Marsh[1] is intimately associated with Skokie Stream, a small, sluggish stream beginning west of Waukegan, Ill., and extending southeast to a point west of Glencoe, Ill. Because of interference by cultivation and by drainage, the areal limits of the marsh can be defined only arbitrarily. As shown in the accompanying map (fig. 1), however, Skokie Marsh is approximately 12 km. long and at its southern end becomes 1.5 km. wide.

In early postglacial times, the marsh was an embayment (ATWOOD and GOLDTHWAIT **1**, p. 58), which later subsided, giving place to a system of drainage. At present the surface soil almost throughout the marsh consists of a black muck or partially decayed peat, 1 m. or less in thickness. Underneath is a subsoil of glacial clay.

General features of the marsh vegetation

Upon analysis, the vegetation at Skokie Marsh is found to consist of three rather pronounced formations.[2] Along the course

[1] For many additional data and photographs of Skokie Marsh, see BAKER (**2**).

[2] The words "formation" and "association" are used throughout this paper in the sense accepted by WARMING (**16**).

taken by Skokie Stream, the plants constitute distinctly a reed swamp formation (fig. 2). Extending along on either side of the reed swamp is a broad level expanse, intermediate between reed swamp and meadow. This may be designated swamp meadow (fig. 3). At the outer edges of the swamp meadow, in narrow areas that have not been too much disturbed by cultivation, true meadow

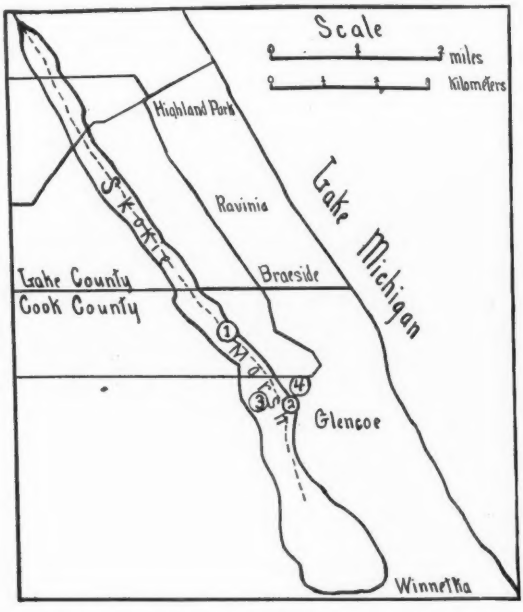

FIG. 1.—Map of Skokie Marsh; the dotted line represents Skokie Stream

is commonly present. At certain places, however, there is an abrupt transition from swamp meadow to forest.

In the reed swamp the plants belong to five easily recognized associations. Where the stream is deepest (as in fig. 2), aquatic or amphibious species, such as *Myriophyllum humile*,[3] *Ranunculus delphinifolius*, and *Potamogeton* (*zosteraefolius?*), are common near the center. In the shallower parts, the species are supple-

[3] All plant names given in this paper conform with the nomenclature of GRAY'S Manual, 7th ed., 1908.

mented or replaced by *Polygonum Muhlenbergii*, *P. hydropiperoides*, *Veronica Anagallis-aquatica*, *Radicula aquatica*, *Sium cicutaefolium*, *Sparganium eurycarpum*, *Glyceria septentrionalis*, *Alisma Plantago-aquatica*, *Rumex verticillatus*, *Callitriche heterophylla*, and *C. palustris*. As *Polygonum hydropiperoides* and *Sium cicutaefolium* are among the most abundant stream plants and appear to be dominant, we may classify the plants growing in the stream or upon its bed,

FIG. 2.—Skokie Stream at point west of Braeside, looking north; July

except along the margins, as the *Sium-Polygonum* association; using SCHOUW's method of nomenclature (SCHOUW **14**, pp. 148–150), we shall call this the *Sio-polygonetum*. On either side of the Sio-polygonetum a narrow or sometimes broad girdle[4] of *Nymphaea advena* and *Castalia odorata* occurs in many places along the stream. Usually these species are accompanied by species characteristic of the Sio-polygonetum; but the soil and light conditions present in

[4] The word "girdle" is here equivalent to the "zones" of many recent authors, and conforms with the recent proposal of FLAHAULT and SCHRÖTER (**5**), except that it is here used for "bands" that are not "concentric."

the girdles of *Nymphaea* and *Castalia* are peculiar to them and justify their treatment as a separate association, the *Nymphaeetum*. Landward from the Nymphaeetum are found dense and either intermixed or almost pure growths of *Typha latifolia*, *Sparganium eurycarpum*, *Scirpus fluviatilis*, and *S. validus*. Scattered to a varying extent among these species are *Sagittaria latifolia* and *Sium cicutaefolium*. Here and there are a few isolated patches of *Dulichium arundinaceum* and of *Decodon verticillatus*. This

FIG. 3.—Skokie Stream at point west of Glencoe, looking south; July

association will be referred to as the *Scirpo-typhetum*. Then again, in certain parts of the reed swamp, at stations slightly less hydrophytic, *Phragmites communis* is prominent. It forms exceedingly compact, nearly pure colonies that may reasonably be treated as an association, the *Phragmitetum*. Finally, we must mention the many large but somewhat scattered patches of *Iris versicolor* and *Acorus Calamus*, occurring in the outer parts of the reed swamp and often extending into the swamp meadow formation. These constitute an association of a very definite stamp, the *Iridoacoretum*.

A general comparison of the reed swamp associations shows that in the Sio-polygonetum and Nymphaeetum, where hydrophytism is greatest, the dominant plants are dicotyledonous. In fact, of the 15 species found to any appreciable extent in these two associations, the 10 most abundant (*Sium*, *Polygonum hydropiperoides*, *P. Muhlenbergii*, *Nymphaea*, *Castalia*, *Rumex*, *Veronica*, *Myriophyllum*, *Callitriche palustris*, and *C. heterophylla*) are dicotyledons.[5] In the other three associations the most abundant species are chiefly monocotyledons.

The swamp meadow differs from the reed swamp in being more uniform, due to greater parallelism between the water table and the soil surface, and does not admit of logical subdivision into associations. The plants are principally such grasses as *Calamagrostis canadensis*, *Glyceria nervata*, *Phalaris arundinacea*, *Poa triflora*, *Sphenopholis pallens*, and *Agrostis perennans*. These are frequently interspersed with *Carex lupuliformis*, *C. vesicaria monile*, *Scirpus atrovirens*, and *S. Eriophorum*. The swamp meadow is used by farmers of the district for the production of marsh hay, and many of them customarily burn over the areas in late autumn. Most of the shrubs and young trees are killed in this way, and so forest development is hindered. Trees occur only in small groups, consisting chiefly of *Salix* (*S. nigra* and other species), *Fraxinus americana*, and *Populus tremuloides*. Frequently associated with these are such shrubs as *Cornus stolonifera*, *Cephalanthus occidentalis*, and *Sambucus canadensis*.

Throughout the reed swamp and swamp meadow are many species which, though very abundant, share only to a small extent in giving to the several associations their distinctive appearance. Thus, *Ludwigia palustris*, *Proserpinaca palustris*, *Penthorum sedoides*, and *Stenophyllus capillaris* are low in habit and obscured by taller plants in the shade of which they may thrive. Again, *Aster Tradescanti*, *Boltonia asteroides*, *Lobelia cardinalis*, *Teucrium occidentale*, and *Scutellaria galericulata*, while extremely common, are nevertheless conspicuous only during the latter part of the summer. The names of such species will be given in this paper only where occasion demands.

[5] See HENSLOW (7), however, regarding the supposed monocotyledonous nature of *Nymphaea* and *Castalia*.

The meadow formation, as already stated, is narrow and more or less interrupted. The soil surface slopes mildly upward, away from that of the swamp meadow. The vegetation is much diversified at different places and from month to month during the vegetative season. *Poa pratensis* and *Agrostis alba* are the dominant grasses, but *Danthonia spicata* and *Agropyron caninum* are frequent. Scattered among the grasses are *Carex stipata*, *C. vulpinoidea*, *C. scoparia*, and *Eleocharis palustris*. In some parts of the meadow *Viola cucullata*, *Senecio aureus*, and *S. Balsamitae* are conspicuous in May and June, while later such species as *Lilium canadense* and *Rudbeckia hirta* are the most noticeable.

In the entire marsh there were found, exclusive of shrubs and trees, 163 species of pteridophytes and spermatophytes. Of these, 68 were common or even abundant.

Certain ecological factors

Four Livingston atmometers were set out May 21, 1911, at different stations indicated in fig. 1. Readings were taken weekly from May 21 to October 15, and afterward corrected according to the method outlined by LIVINGSTON (**9**, p. 273, and **11**).[6] A detailed account of the evaporation data thus obtained may be published subsequently elsewhere, but only the general results will be given here. It was found that the average daily evaporation at station 1 (in the center of the reed swamp) for the 147 days was 3 cc.; at station 2 (in the outer part of the reed swamp), 4.5 cc.; at station 3 (in the swamp meadow), 4.27 cc.; and at station 4 (in a stretch of forest running along the east side of the marsh and composed chiefly of *Quercus bicolor* and *Fraxinus americana*), 7.91 cc. Thus it will be seen that the evaporation rate was lowest in the reed swamp; that the evaporation rates in the reed swamp and the swamp meadow were closely similar; and that these rates were from about 38 per cent to about 57 per cent as great as the rate in a neighboring forest of *Quercus bicolor* and *Fraxinus americana*.

[6] The unglazed portion of each cup was placed at a mean height of 2.5 dm. above the soil surface. The instruments were not provided with a rain-excluding device, such as that recommended by LIVINGSTON (**10**).

From September 3 to October 22, 1911, weekly readings were taken of the rates of evaporation at different levels above the soil surface. Among the plants of *Phragmites*, four atmometers were placed at levels ranging from 0 m. to 1.95 m. above the soil. The average daily rate for the seven weeks at 1.95 m., or near the top of the *Phragmites* plants, was found to be 7.5 cc., just three times as great as the average daily rate of 2.5 cc., at the surface of the soil. Similar results were obtained with five atmometers in a dense growth of *Typha*. In each case the data secured are found to support YAPP's important contention (**20**) that for species growing side by side, but vegetating mainly at different heights, the conditions of growth may be very unlike.

The depth of the water table in the reed swamp and the swamp meadow was observed each week from May 21 to October 22, 1911. The water in Skokie Stream was about 1 m. deep in May; its depth then gradually decreased until in July, when the stream bed was in most places fairly dry; in August the water began to rise again, and by October had reached an average depth of about 1.1 m. In the rest of the reed swamp and in the swamp meadow the water table during May was coincident with or above the soil surface; in early September it sank to the maximum depth of 1 m. in the reed swamp and 1.75 m. in the swamp meadow; and then, rising rapidly, reached the surface again by the middle of October. According to farmers in the vicinity of Glencoe, Skokie Stream has sometimes in the past risen until a depth of about 3 m. was reached; in such cases the entire marsh was of course deeply submerged. Various attempts have been made to classify the constituent species of a formation with relation to the optimum water table depth for each species. But where the water table varies greatly in depth from month to month and from year to year, data must be secured through many years if they are to show more than merely the relative degrees of hydrophytism to which plants in different places are subject.

Litmus tests each week, from May 21 to October 22, 1911, showed the water in Skokie Stream to be either neutral or slightly alkaline. Similar tests showed the soil water in the outer parts of the reed swamp and in the swamp meadow to be usually neutral or slightly

alkaline; only for a few days in August was acid present, and then the amount was almost negligible.

Subterranean organs and their interrelationships

A study of the subterranean organs of the reed swamp plants showed that in many cases the depth is roughly proportionate to the depth of the water table. YAPP (**19**) arrived at a similar conclusion concerning the plants at Wicken Fen. And since the depth of the water table may influence the depth of the subterranean

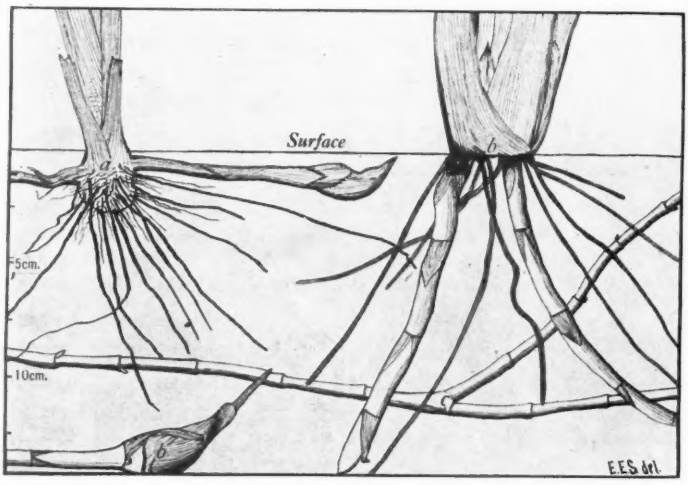

FIG. 4.—*a, Sparganium eurycarpum; b, Sagittaria latifolia; c, Polygonum Muhlenbergii;* July.

organs, the latter in turn may enter as a potent factor into the success or failure of various species. Thus, for example, the rhizomes of *Polygonum Muhlenbergii*, where this species occurs in the Sio-polygonetum, are usually at or near the surface of the stream bed. As KING (**8,** p. 240) and others have pointed out, saturated soil like that of the stream bed does not admit oxygen freely. And so, in the Sio-polygonetum, the rhizomes of *Polygonum* and their roots appear advantageously placed. But in the Scirpo-typhetum (fig. 4), where the surface soil is occupied by an extremely dense mat composed of the rhizomes of *Typha*, *Sparganium*, and

Scirpus, the rhizomes of *Polygonum* average about 10 cm. in depth. Hence in the Scirpo-typhetum, although the rhizomes of *Polygonum* are lower, evidently, in response to the greater average depth of the water table, they gain the additional advantage of being able to travel with less interference from the other rhizome systems.

An examination of *Typha*, *Sparganium*, *Scirpus fluviatilis*, and *S. validus* shows these species to be very similar in growth-form and hence capable of keen competition. Where any one of these species becomes more abundant in the Scirpo-typhetum, the others become less so. Because of the thick, strong rhizomes, the subterranean competition is to some extent mechanical; but, as CLEMENTS (**3**, pp. 285–289) maintains, it is probably to a much greater extent physiological (or "physical"), especially in the case of the roots proper. The opposition that any or all of these species can offer to the intrusion of other species makes their hold upon the soil very effective. With *Sagittaria* (fig. 4), however, the case is different. Its growth-form favors a less compact arrangement of the individual plants. Its rhizomes cannot produce a thick mat. Obviously, as the plants of *Sagittaria* are developing vegetatively, other species, such as *Typha*, *Sparganium*, and *Scirpus*, may easily invade and occupy the soil with their densely matting rhizomes. Subsequently the rhizomes of *Sagittaria*, if they are to establish new plants at proper distances away from the parent plant, must either plough their way along through the surface mat of rhizomes or travel underneath. They usually do the latter. As a rule several rhizomes start growth from each plant in early summer, in a downward direction; at a depth of 10–15 cm. they assume a horizontal direction for some distance; they then grow upward again, with a tuberous, propagative thickening near the distal end, and finally resemble somewhat a shallow, inverted arch.[7] Thus interference from surface rhizomes and roots is to a great extent avoided. In this case, then, while it is not certain that the inverted arch of the *Sagittaria* rhizome is a direct adaptation to this particular struggle, it is certain that the inverted arch, however induced originally, is here of the greatest value.

[7] For illustrations of the similar rhizomes of *Sagittaria sagittifolia* see GLÜCK (**6**, *pl. 6* and *figs. 35* and *39*).

PIETERS (**13**) found among the plants of western Lake Erie that even where *Sagittaria latifolia* was most abundant, *Sparganium* (and *Zizania*) had secured a foothold. On the other hand, throughout all the broad "zones" of *Sparganium*, *Scirpus validus* ("*S. lacustris*"), and *S. fluviatilis* that he describes, he says *Sagittaria latifolia* was common.

A study of the subterranean organs of *Sagittaria*, *Sparganium* (or *Typha* or *Scirpus*), and *Polygonum* shows that because of differences in direction or in depth they conflict but little. Again, because of differences in growth-form, their aerial parts do not conflict seriously. Thus a given area can usually support a greater mass of vegetation if these three growth-forms be present in fair mixture than if only one be present. SPALDING (**15**) has described the mutual relationships of *Cereus giganteus* and *Parkinsonia microphylla*, two desert species which thrive together because the occupation of different depths by their root systems enables them "to utilize to the utmost the scanty rainfall." WOODHEAD (**18**) found *Holcus*, *Pteris*, and *Scilla* forming a non-combative "society or sub-association." For a group of plants mutually competitive, WOODHEAD uses the term "competitive association." Recently WILSON (**17**) likewise speaks of a "complementary association" or "society." But the use of the words "association" and "society" in this connection is unfortunate. These words have already been used by COWLES (**4**) and others (see WARMING **16**, p. 144) to denote a primary subdivision of a formation. As will be seen later (and in fact as WOODHEAD'S use interchangeably of "sub-association" and "association" would imply), not all complementary or competitive groups are coextensive with a true association. We shall here substitute the word community, which is of less restricted application. Thus, *Sagittaria* and *Polygonum*, where occurring in the Scirpo-typhetum with either *Typha* or *Scirpus fluviatilis* or *S. validus*, constitute a complementary community. But *Sparganium*, *Typha*, *Scirpus fluviatilis*, and *S. validus*, where they occur intermixed, form a competitive community.

Species that are complementary in one association may be less so in another. Thus, *Polygonum Muhlenbergii* and *Sparganium* are complementary in the Scirpo-typhetum; but in the Sio-

polygonetum, where their rhizomes lie in common near or at the surface of the stream bed, they are "edaphically" (see WOODHEAD **18**) competitive, and hence complementary only in an aerial way. In this particular case, however, the frequently open appearance of the vegetation in the Sio-polygonetum indicates that the mutual biotic struggle of the two species is less keen than their separate struggles against somewhat adverse environmental conditions.

In the reed swamp certain mints become conspicuous during midsummer, particularly so in the Scirpo-typhetum, where they thrive in the shelter of *Typha* and other tall plants. *Teucrium occidentale* and *Scutellaria galericulata* are very common. They produce from their basal nodes numerous slender stolons that run out at different depths in the soil, and these stolons may produce new plants. These species tend to have their root systems 3–6 cm. lower in wet situations than in dry, although exceptions to this rule are not rare. But whether growing from plants in dry or from those in wet situations, the new stolons exhibit a remarkable power of changing their direction of growth, in response to numerous obstructions, and thus they may proceed further without serious results. Considering the strength and size of the rhizomes of *Typha*, *Sparganium*, and *Scirpus*, also the delicate nature of the stolons of *Teucrium* and *Scutellaria* and their capacity for altering growth-direction, it is probable that mechanical competition between such rhizomes as those of *Typha* and such stolons as those of *Teucrium* is practically absent. Again, the aerial parts of the *Typha* form vegetate chiefly in higher atmospheric strata than do those of the *Teucrium* form. Evaporation readings show that in the higher strata evaporation is much greater. And while plants of relatively xerophytic structure (e.g., *Typha*, *Sparganium*, and *Scirpus*) are fitted to withstand acute drying conditions, plants with foliage of looser texture (e.g., *Teucrium* and *Scutellaria*) can vegetate better in lower strata where the effect is that of greater humidity; the abundance of the latter plants among the former at Skokie Marsh tends to confirm this statement. Further, the persistence with which tall plants like *Typha* become dominant under favorable soil conditions shows that they are not, at least noticeably, harmed by plants like *Teucrium*. If, finally, we allow for the great avail-

ability of nitrogenous foods in the soil and for the differences in food requirements, it becomes clear that the numerous communities of *Typha* and *Teucrium*, *Typha* and *Scutellaria*, *Sparganium* and *Teucrium*, etc., are complementary.

The purity of the Phragmitetum has already been mentioned. Many species that flourish elsewhere in the reed swamp under a wide range of light, moisture, and other shelter conditions fail to thrive here. Only *Calamagrostis canadensis* gains noticeable

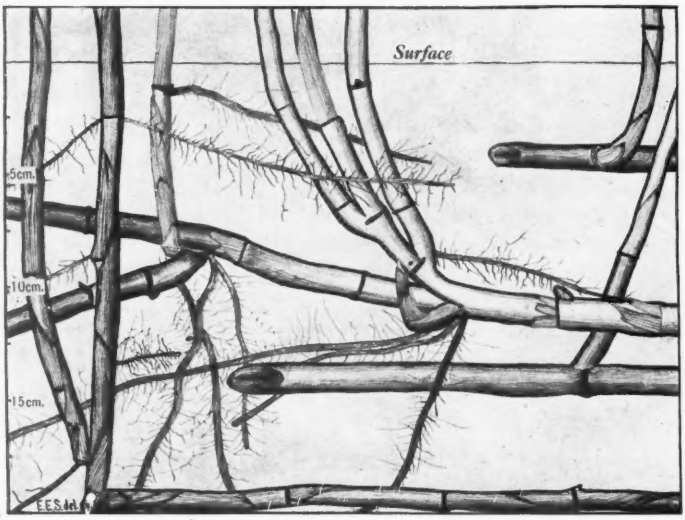

FIG. 5.—*Phragmites communis;* July

entrance, and then imperfectly. The dead *Phragmites*' growth of previous years makes a considerable but loose covering near the soil, its decay not being facilitated as in the Scirpo-typhetum, where water is more abundant. This dead cover may perhaps act as a partial check upon the invasion of other species. But a study of the rhizomes of *Phragmites* (fig. 5) shows another fact which probably is more important. They do not occupy one particular level, but rather several different levels of soil. As a result, there is formed a dense mat of rhizomes and roots, about 2.5 dm. deep. Obviously, the subterranean organs of other species which might

start growth here must compete with the extraordinarily large number of *Phragmites* roots and rhizomes. Where other factors are suited equally to *Phragmites* and to competing species, this biotic factor in the subaerial struggle ought usually to decide in favor of *Phragmites*.

The Nymphaeetum displays many complementary communities. The rhizomes of *Nymphaea advena* (fig. 6) are usually

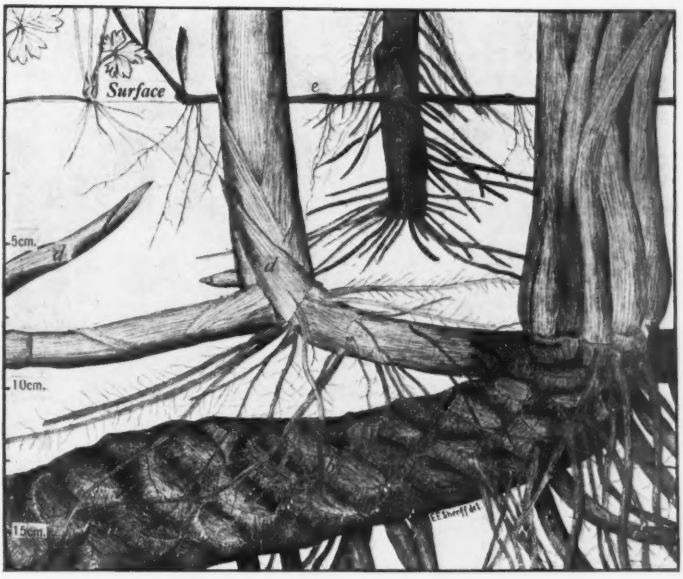

FIG. 6.—*a, Ranunculus delphinifolius; b, Nymphaea advena; c, Sium cicutaefolium; d, Typha latifolia; e, Polygonum hydropiperoides;* drawn in early July.

5–10 cm. thick and lie mostly at a depth of 8–25 cm. below the soil surface. The rhizomes of *Castalia odorata*, while smaller, lie at a similar depth. Where the Nymphaeetum intergrades with the Scirpo-typhetum, as is commonly the case, the rhizomes of *Typha*, *Sparganium*, and *Scirpus validus* lie higher in the soil. In many places the soil surface itself is occupied by the stolons of *Ranunculus delphinifolius* and the creeping stems of *Polygonum hydropiperoides*, with a large, upright stem base of *Sium cicutaefolium* present here

and there. In other places, *Ranunculus* is replaced by *Myriophyllum humile* or by young plants (growing chiefly from detached leaves) of *Radicula aquatica*, while *Polygonum* is replaced by *Veronica Anagallis-aquatica*, and *Sium* by *Rumex verticillatus*. And while it is true that *Nymphaea* and *Castalia*, or *Typha* and *Sparganium* and *Scirpus*, or *Ranunculus* and *Myriophyllum* and *Radicula*, or *Polygonum* and *Veronica*, or *Sium* and *Rumex* are mutually competitive, yet a complete community (as shown, e.g., in fig. 6) is complementary; the basal parts chiefly because of different depths, and the upper parts chiefly because of different growth-forms.

An inspection of the Nymphaeetum shows that only where *Nymphaea* is nearly or quite absent does *Sagittaria latifolia* successfully invade from the Scirpo-typhetum. As is commonly known, the rhizomes of *Nymphaea* in many habitats are usually decayed to within a short distance of the growing apex. An investigation during August 1911 showed that generally where the rhizomes of *Sagittaria* had penetrated these decayed parts, they themselves had started to decay.[8] Frequent cases were found where the decayed *Nymphaea* rhizomes lay nearer the surface and the *Sagittaria* rhizomes had proceeded underneath, unharmed. Speaking in a general way, while *Nymphaea* and *Sagittaria* thrive better in the Nymphaeetum and Scirpo-typhetum respectively, yet along the line of tension between these two associations the injury done by the decayed *Nymphaea* rhizomes to the rhizomes of *Sagittaria* is a factor that appears to be decisively in favor of *Nymphaea*. The inverted rhizome arch of *Sagittaria*, useful in the Scirpo-typhetum, is here more often harmful.

In many parts of the Irido-acoretum, *Polygonum Muhlenbergii* and *Galium Claytoni* abound, and these form with *Acorus* a complementary community (fig. 7). The creeping stems of *Galium* root upon the soil surface, the rhizomes of *Acorus* lie just beneath, and those of *Polygonum* are deepest of all. The bushy shoot of *Galium* appears not to harm the slender, ensiform leaves of *Acorus*, and

[8] Many litmus tests uniformly showed the decayed parts of the *Nymphaea* rhizomes to be strongly acid. Enough cultural experiments have not been performed, however, to determine whether the effect upon the *Sagittaria* rhizomes, as above noted, is due to acid or to other causes.

they in turn do little harm to it. In late summer, the shoots of *Polygonum* rise above those of *Acorus* and *Galium* without apparent harm to either of them. And while *Polygonum* might increase in abundance if *Acorus* and *Galium* were entirely absent, still to a great extent the community, viewed as a whole, is complementary. Elsewhere in the Irido-acoretum the rhizomes of *Acorus* are replaced by those of *Iris;* and very often the rhizomes of *Galium* are replaced by those of *Ludwigia palustris*, *L. polycarpa*, *Proserpinaca*

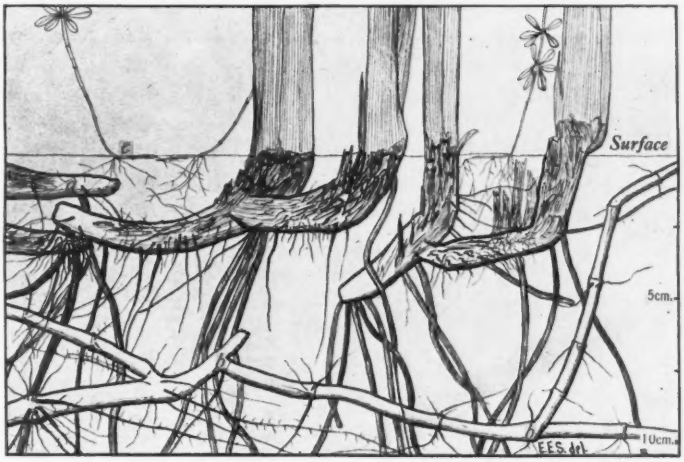

FIG. 7.—*a, Acorus Calamus; b, Polygonum Muhlenbergii; c, Galium Claytoni;* July

palustris, *Penthorum sedoides*, *Veronica scutellata*, or *Campanula aparinoides*.

The basal parts of the various swamp meadow species are usually more slender than those of the reed swamp species, and hence the texture of the surface mat of rhizomes, roots, etc., is finer. Then, too, reproduction by seeds becomes more common. *Polygonum Muhlenbergii* is present in the swamp meadow, and by means of its extensively creeping rhizomes, which lie rather low, it forms in some places large patches. Certain other perennials, e.g., *Asclepias incarnata* and *Sium cicutaefolium*, which root near the surface, may reproduce largely by seed or by new shoots arising from the old stem base of the preceding year. In the middle

and latter parts of the summer, when the surface soil is no longer saturated with water, such annuals as *Panicum capillare*, *Echinochloa Crus-galli*, *Eragrostis hypnoides*, *Stenophyllus capillaris*, *Polygonum Persicaria*, *Amaranthus paniculatus*, and *Erechthites hieracifolia* take possession of all exposed surface soil and become exceedingly abundant. Much of the surface soil that has been denuded by burning or by other causes is already occupied, however, by the rhizomes of perennials such as *Ludwigia palustris*, *L. polycarpa*, *Proserpinaca palustris*, etc. In these cases *Boltonia*

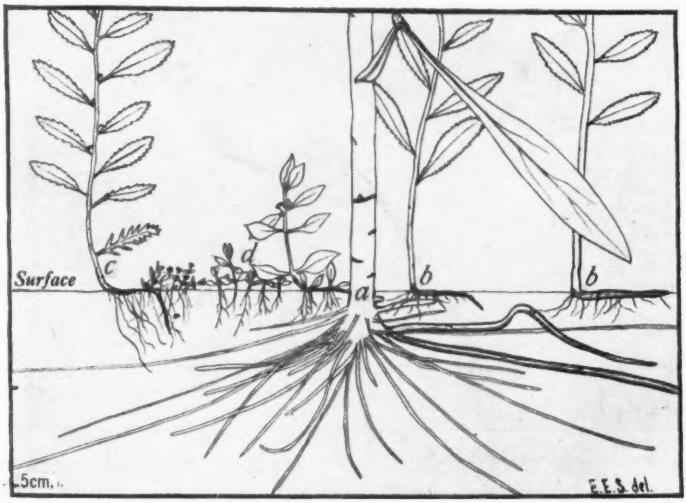

FIG. 8.—*a*, *Boltonia asteroides*; *b*, *Penthorum sedoides*; *c*, *Proserpinaca palustris*; *d*, *Ludwigia palustris*; *e*, *Callitriche palustris*; July.

asteroides, *Callitriche heterophylla*, and *C. palustris* are often abundant; both species of *Callitriche*, however, die away in midsummer, becoming replaced by annuals. Fig. 8 shows such a community. *Callitriche*, maturing earliest, is "seasonally" (WOODHEAD **18**) complementary with the other species. *Boltonia* roots lowest, while its aerial shoot grows much the highest; and since it is not harmed very much by *Proserpinaca*, *Ludwigia*, and *Penthorum*, while they derive, if anything, benefit from its shelter, *Boltonia* is complementary both aerially and subaerially. *Proserpinaca*,

Ludwigia, and *Penthorum* are very similar throughout in growth-form and they constitute mutually a competitive community. But, even though mutually competitive, they form with *Boltonia* and *Callitriche* a community that may properly be called complementary.

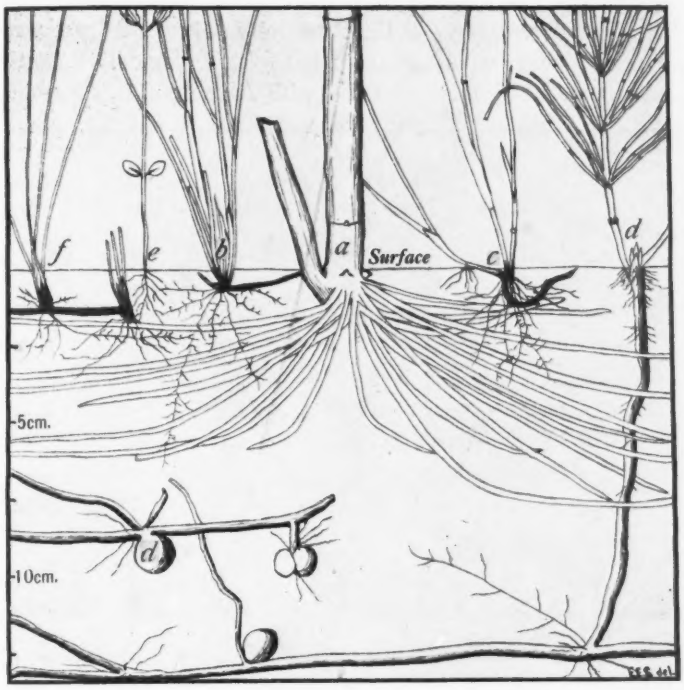

FIG. 9.—*a, Asclepias incarnata; b, Poa pratensis; c, Agrostis alba; d, Equisetum arvense; e, Acalypha virginica; f, Eleocharis palustris;* July.

As has already been stated, the flora of the meadow is highly diversified. A very large number of definite interrelationships, similar to those detailed for the reed swamp and the swamp meadow, are found to exist, but lack of space precludes more than a brief description of a few examples. In the moist parts of the meadow, the soil at a depth of 3–12 cm. frequently contains the tuberous thickened roots of *Cicuta maculata* and *Oxypolis rigidior*, also the

tuber-bearing rhizomes of *Equisetum arvense*. In drier situations the bulbs of *Lilium canadense* occur at a similar depth (most often about 10 cm. deep). Higher in the soil may be found (fig. 9) roots of such species as *Asclepias incarnata*, *Thalictrum revolutum*, and *Lathyrus palustris*, while the surface soil contains a mixture of the root systems of *Poa pratensis*, *Agrostis alba*, *Eleocharis palustris*, *Acalypha virginica*, etc. In the community shown in fig. 9, *Equisetum* is edaphically complementary, but (considering only the aerial sterile shoots) aerially competitive with *Poa*, *Agrostis*, *Eleocharis*,

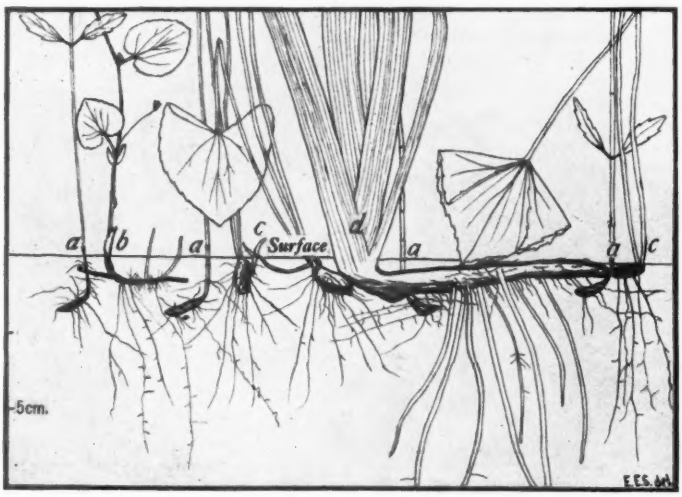

FIG. 10.—*a*, *Lycopus americanus; b*, *Viola conspersa; c*, *Viola cucullata; d*, *Iris versicolor;* July.

and *Acalypha*. To a moderate extent, the plants rooting near or at the surface appear to be complementary with the plants rooting deeper.

Small, apparently open depressions are numerous in the moist parts of the meadow. These generally contain (fig. 10) such plants as *Iris*, *Acorus*, *Viola conspersa*, *V. cucullata*, *Cardamine bulbosa*, and seedlings of *Lycopus americanus*. And while the rhizomes of *Cardamine* and *Lycopus* occur almost invariably just below those of the other species, and while the different species doubtless make

different demands upon the soil, yet edaphic competition is undoubtedly sharp. The almost complete absence, in these small areas, of stoloniferous or loosely spreading species makes it seem certain that there exists some mechanical competition in which species of compact and frequently caespitose habit or species capable of reproducing extensively from seed are successful. The extent, however, to which their success is achieved because of their growth-form or because of their superior adaptation to the particular complex of soil and moisture conditions in these small areas is of course incapable of accurate estimation without further study. The idea of mechanical competition (i.e., a struggle either among the various species because of the mutual bodily resistance of any or all of their growing parts, or of individual species because of the resistance offered by the soil's compactness to the locomotion of their subterranean organs) is opposed by CLEMENTS (**3,** pp. 285–289); but WARMING (**16,** p. 324), in accounting for the usual absence of vegetative locomotion among perennial herbs of the meadow formation, seems inclined to accept this idea in part.

Summary and conclusions

1. Atmometer readings, taken for seven weeks at four different levels among *Phragmites* plants and at five different levels among *Typha* plants, show that among marsh species of compact social growth evaporation is proportionate to the height above the soil. These results thus coincide with those of YAPP (**20**).

2. Data accumulated at Skokie Marsh appear to support the conclusion of MASSART (**12**) that it is a matter of importance to perennial plants that their hibernating organs occupy a definite level in the soil.

3. Certain observed cases of variation in this level (*Teucrium occidentale*, *Polygonum Muhlenbergii*, etc.), corresponding to changes in the water level, indicate that with certain species, at least, the depth of the water table is much the most potent controlling factor.

4. Two or more species may live together in harmony because (1) their subterranean stems may lie at different depths; (2) their roots may thus be produced at different depths; (3) even where roots are produced at the same depth, they may make unlike

demands upon the soil; (4) the aerial shoots may have unlike growth-forms; or because (5) even where these growth-forms are similar, they may vegetate chiefly at different times of the year. According as one or more of these conditions control the floristic composition of a given community the community may be called complementary.

5. The root depth having been determined by various factors for the different species in a community, the specifically different root systems then function in a complementary or a competitive manner as the case may be. But even if the root systems be complementary, the community may be competitive because of marked competition among the aerial parts. Likewise, competitive root systems may render competitive a community otherwise complementary.

6. Through the ability of certain species to utilize different strata in the soil, the aerial portions of these plants are brought into a closer competition. And with closer competition, the chances in the past for further adaptation of similar aerial shoots to dissimilar growth conditions must have been greatly increased. Hence communities, formerly complementary in a purely edaphic way, may have been largely instrumental in the evolution of completely complementary communities. In so far as they have been thus instrumental, the fact deserves great emphasis, especially when we consider the far-reaching changes in form and anatomical structure necessarily developed as a prerequisite to living in a completely complementary community.

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BRIEFER ARTICLES

ABNORMALITIES IN PROTHALLIA OF PTERIS LONGIFOLIA

(WITH FOUR FIGURES)

Some abnormal conditions in archegonia were noted in prothallia, probably of *Pteris longifolia*. The spores had been sown about the middle of October, on moist sphagnum in a low jar covered with a glass plate. The resulting prothallia, after three weeks, were partly used in class work. Those remaining after class use were put aside for further development, in the hope of getting material for histological preparations. No particular care was taken to keep conditions constant or normal. The moisture varied greatly at times, and the temperature was a very variable factor, since for some time the jar was kept on the sill of a none too tight east window. As a result of some extremely cold weather, it was removed to a less exposed position on a shelf, somewhat darker than that on the window sill. In January the material was killed and fixed in 0.6 per cent chromacetic acid, washed, dehydrated, and imbedded in paraffin. The sections were cut 5 μ thick. Safranin and gentian violet were principally used in staining.

The prothallia were unusually small, and in sections the sex organs appeared smaller than is usual in *Pteris*. In spite of many normal archegonia, 8 cases were found in about 35 prothallia where there were more than two neck canal cells. In 5 of these, there were definitely and certainly four such nuclei, either arranged in a row, as in fig. 1, or grouped closely together near the mouth of the canal. In the other cases, the condition of the nuclei was such that it could not be ascertained whether the number was three or four. The four-nucleate neck canal cell has been reported for Filicineae by Miss TWISS[1] in *Lygodium circinatum*, where occasionally this condition occurs instead of the usual two neck canal nuclei.

A second abnormality which occurred in these prothallia is shown in fig. 2. Here there are evident two eggs, two ventral canal cells, and the usual two neck canal nuclei. This condition has been reported for

[1] TWISS, EDITH MINOT, The prothallia of *Aneimia* and *Lygodium*. BOT. GAZ. 49:168–181. *pls. 10, 11*. 1910.

Adiantum cuneatum by Miss LYON,[2] and again by Miss FERGUSON[3] in *Pteris*, probably *P. cristata*. Unlike the case cited by Miss FERGUSON, the basal cell did not give rise to the second egg and ventral canal cell, but had divided periclinally into approximately equal cells. In some other archegonia a similar periclinal division gave rise to two unequal cells, not strikingly different in proportions from an egg and ventral canal cell, but not having the characteristic granular appearance of such.

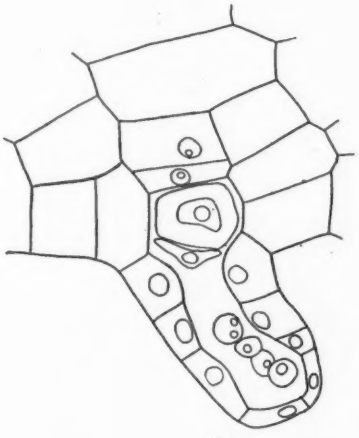

FIG. 1

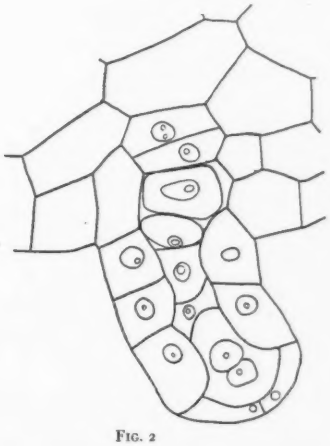

FIG. 2

FIGS. 1, 2.—Fig. 1, archegonium of *Pteris longifolia*, showing four neck canal nuclei; ×500; fig. 2, archegonium in which two eggs and two ventral canal cells have been formed; the basal cell has divided periclinally; ×500.

A third unusual condition, of which no former report has come to hand, is one in which a definite wall has been formed between the two neck canal nuclei, giving two neck canal cells. This preparation is shown in fig. 3. The cells are practically equal in size and very similar, or one might be led to believe that this is an early stage in the development of such an archegonium as shown in fig. 2. In this archegonium the basal cell appeared to have divided unequally in a periclinal direction.

[2] LYON, FLORENCE M., Evolution of the sex organs. BOT. GAZ. **37**: 280–293. *figs. 16*. 1904.

[3] FERGUSON, MARGARET C., Imbedded sexual cells in the Polypodiaceae. BOT. GAZ. **51**: 443–448. *pls. 26, 27*. 1911.

Although sporophytes were rarely found in the material used, one appeared in which an entire quadrant, the foot, had failed to develop. In another prothallium, there was a structure which appeared to be an apogamous sporophyte.

An antheridium, in which the basal cell has apparently given rise to spermatogenous tissue, is shown in fig. 4. The cap cell and ring cells appear normal, except for an unusual slope of the walls. Unfortunately

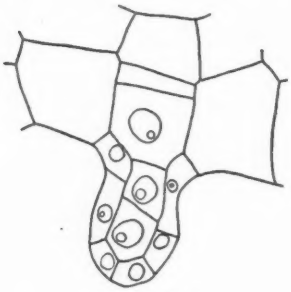

FIG. 3

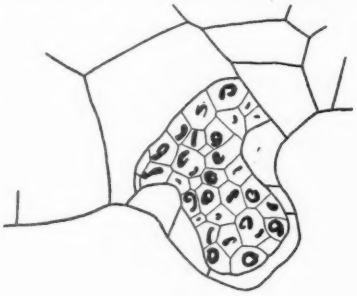

FIG. 4

FIGS. 3, 4.—Fig. 3, archegonium showing a definite wall between the two neck canal nuclei; ×500; fig. 4, antheridium in which the basal cell has given rise to spermatogenous tissue; ×500.

the section figured was the last on the slide, so that the structure could be traced in one direction only.

The writer is indebted to Professor JOHN M. COULTER and Dr. W. J. G. LAND for suggestions in this work, and also to Mr. LOREN C. PETRY, who kindly turned over his excellent preparations made from this material.—NORMA E. PFEIFFER, *The University of Chicago.*

SIR JOSEPH DALTON HOOKER

(WITH PORTRAIT)

The recent death of Sir JOSEPH DALTON HOOKER, at the advanced age of nearly 95 years, removes from the ranks of living botanists one of the most distinguished scientific men of our times; his long, continuous, and active career of over 70 years in the botanical field has been equaled by few men. JOSEPH DALTON HOOKER was born June 30, 1817, at Halesworth, Suffolk, England, and died December 10, 1911, at his home near London. The son of an eminent botanist, living in a scientific

atmosphere, it was but natural that his life work should be in botany rather than in the medical profession for which he was educated primarily, having taken the degree of M.D. at the University of Glasgow in 1839.

HOOKER'S botanical work began in his father's herbarium, and his early interests were mainly in the lower groups of plants, particularly the mosses. In 1837, at the age of 20, he published his first contribution to botanical literature. Two years later he was commissioned botanist to the Antarctic Expedition under the command of Sir JAMES CLARK ROSS, and in this capacity acquired in a comparatively short time an extensive knowledge of the floras of the south temperate and sub-antarctic regions; the results of this expedition were embodied in six large quarto volumes under the general title of *The botany of the Antarctic voyage of H.M. discovery ships Erebus and Terror in the years 1839–1843 under the command of Captain Sir James Clark Ross*, published 1844–1860. Although HOOKER had concerned himself chiefly with the lower groups of plants, yet he early developed an interest in fossil botany, and this interest was fostered by the appointment in 1845 to the position of botanist to the Geological Survey of Great Britain; he remained in the service of the survey for about two years and made important contributions to paleobotanical literature.

The desire for a more extended knowledge of the flora of the Old World tropics led HOOKER to organize a botanical expedition to India. The project received recognition and favor, and accordingly he entered this little known field in 1848. Some of the results of his early observations in India were published in *The Himalayan journals* and in a single volume under the title of *Flora Indica*, the latter work being collaborated with Dr. THOMAS THOMSON and issued in 1855. In this year HOOKER

was appointed assistant director of the Royal Botanic Gardens at Kew, a position which he held for ten years. It was a decade of extraordinary activity in botanical exploration and in the study of herbarium collections; and it was during this time that the preparation of a comprehensive and much needed work on the genera of plants was formulated, and happily the elaboration of the *Genera plantarum* was undertaken in collaboration with Mr. GEORGE BENTHAM, and a part of the first volume of this monumental work appeared in 1862.

Upon the death of Sir WILLIAM JACKSON HOOKER, the eminent director of the Kew Gardens, JOSEPH DALTON HOOKER succeeded to the directorship, and this post he most successfully occupied for about 20 years. During this time vast improvements were made at the Gardens, the collections at the Kew Herbarium were greatly augmented, important publications were completed, notably the *Genera plantarum*, and others were continued; but with all the onerous duties of this important office time was found for further botanical explorations in various parts of the world. In 1877 HOOKER visited the United States, and in company with Dr. ASA GRAY an expedition was made across the continent to California; the results of this journey were incorporated in a joint paper by GRAY and HOOKER which appeared in 1881.

In 1885 HOOKER retired from the directorship of Kew, but from that time until shortly before his death he continued actively but privately in independent taxonomic research. By far the greater amount of HOOKER'S published work (and the number of titles exceeds 200) has been in floristics. Because of his comprehensive knowledge of botany and his broad conception, his productions have been masterly; but his constant interest in plant distribution and his numerous writings on this subject are of such a character as justly to give him the rank of an authority in this field. In fact it may be said that HOOKER was here at his best. His papers on the geographical distribution of plants are full of originality, the facts are marshaled in a logical and convincing order, and the subject-matter is written in an attractive style, so that his published papers are among our most suggestive and reliable sources of information in this department of botanical science.

The esteem and high regard in which Sir JOSEPH DALTON HOOKER, as a man and scientist, was held by his contemporaries is indicated by the many honors extended to him by numerous scientific societies and learned organizations both at home and abroad; in several of these he took an active part for the attainment and advancement of scientific knowledge.—J. M. GREENMAN, *Chicago*.

CURRENT LITERATURE

BOOK REVIEWS

Heredity

Several courses of public lectures on heredity have been made the basis of a very readable book by CASTLE,[1] in which the principles of Mendelian heredity and other related topics are discussed with special reference to their bearing upon evolution and animal breeding. The rapidly increasing number of expositions of Mendelism are warranted both by the growth of scientific knowledge, and by the popular demand for information, and it is gratifying to have the subject presented in easily comprehensible language by one who is among the foremost investigators of the phenomena with which the book deals. The manner of origin of this book makes it natural that the author should illustrate the various principles of heredity by examples from his own extensive experiments, whenever such examples are available, and this method gives the book a unique value.

The brief introductory chapter on "Genetics a new science" recognizes the profound influence exercised by the theory of evolution in many fields of human activity, and shows how the evolutionary idea has forced man to consider his own probable future and to seek to control that future. As the "existence of civilized man rests ultimately on his ability to produce from the earth in sufficient abundance cultivated plants and domesticated animals," "civilization may be advanced in a very direct and practical way" by an increased knowledge of plant and animal breeding. To the solution of the problem "how to create new and improved breeds better adapted to the conditions of present-day agriculture," and especially to an exposition of the "operations" of Mendel's law of heredity, the author specifically addresses himself.

Chap. i on "the duality of inheritance" defines heredity as "organic resemblance based on descent," and discusses fertilization, pointing out that either eggs or sperms can under certain experimental conditions produce a complete organism without union with another gamete, and that such a result is realized regularly in nature in the case of male bees and wasps. The x and $2x$ generations of LOTSY are then considered under the designation N and $2N$ generations, a change of terminology which has nothing to commend it. Chap. ii distinguishes between "germ-plasm" and the body or "soma," and cites experiments in the transplantation of eggs to an alien soma as proof of

[1] CASTLE, W. E., Heredity in relation to evolution and animal breeding. 8vo, pp. xii+184. *figs.* 53. New York: D. Appleton & Co. 1911.

the correctness of WEISMANN'S contention that "body and germ-cells are physiologically distinct," and that "body (or somatic) influences are not inherited." The next six chapters deal with "the greatest single discovery ever made in the field of heredity, Mendel's law," with illustrations drawn chiefly from the author's experiments with guinea-pigs, rabbits, rats, and mice. After a careful statement of the general principles with concrete examples, attention is given to the determination of dominance, heterozygous characters and their "fixation," atavism or reversion, evolution by loss or gain of characters, evolution of new races by variations in the potency of characters, modification of unit-characters by selection, and "blending" inheritance. This enumeration of the subjects treated suffices to indicate that the author's discussion is no merely formal presentation of the ramifications of the Mendelian system. Instead, it deals lucidly and entertainingly with a number of moot questions. It is pleasing to note that the author does not follow some other recent writers (BATESON, PUNNETT, DAVENPORT) in the view that dominance is always due to the presence of a gene which is absent from the recessive form. He mentions several cases for which this explanation is not available, and leaves the problem as to the cause of dominance unsolved. He is convinced that unit-characters may be modified by selection. He says (p. 120): "In several cases I have observed characters at first feebly manifested gradually improve under selection until they became established racial traits." While this must be accepted as an observed fact, the statement that it is due to selection is apt to be misleading. The difficulty remains that selection can only pick out individuals already possessing the observed degree of development of any characteristic under consideration, and does not in any manner modify the qualities which will be possessed by the offspring of the selected individuals. It only permits such individuals to reproduce to the exclusion of other individuals which do not have the character in question. Under "blending inheritance" the now well-known case of skull-size and ear-length in rabbits is discussed, and the view is expressed that in the light of experimental results of NILSSON-EHLE, EAST, and others, such cases of apparent blending may really prove to be segregating inheritance in which a considerable number of units are involved.

In chap. ix the effects of in-breeding are considered, and the reviewer's conception is indorsed, that the apparent deterioration is generally due to the formation of homozygous strains, whereby the stimulus is lost which comes from the "bringing together of differentiated gametes, which, reacting on each other, produce greater metabolic activity." In this connection the statement is made (p. 150) that "under self-pollination for one generation following a cross, half the offspring become homozygous; after two generations three-fourths of the offspring are homozygous"; and so on. This statement is misleading as it stands, and is literally true only in the case of monohybrids. A second cause recognized for deterioration following in-breeding is the appearance of recessive defects, such as albinism, etc., a cause which has been specifically pointed out by DAVENPORT.

The tenth and last chapter deals with heredity and sex. The hypothesis offered by the author several years ago that the female regularly possesses a chromatic element, or something else in addition to the possessions of the male, is made the key to the entire discussion of this subject, and a series of facts is presented which give the hypothesis considerable apparent plausibility, although the philosophical basis for it seems to the reviewer to be a little strained. This basis is found in the statement that the female as compared with the male has an additional function, namely the supplying of nourishment to the young zygote. On the other hand, it may be pointed out that the male differs from the female in many functions, and is in many respects morphologically and physiologically the superior sex, and it is possible to interpret these differences as additions to the female. If the egg has the added function of nourishing the young zygote, the sperm has the added function of motility, and there seems no better a priori ground for expecting an additional chromatin element to represent one of these additions than the other. The reviewer believes that there is no sufficient ground at present for the assumption that sex is always determined in the same manner. It cannot be determined as yet whether the basic differences between the sexes are quantitative or qualitative, and in either case the same results might be attained by any one of several different methods. The attempt to bring the sex-phenomena of all organisms under a single viewpoint is premature.

Each of the chapters is followed by a "bibliography," but the meagerness of the literature lists may be judged from the fact that they include only 46 titles from 26 authors, including 14 of CASTLE'S own papers. This may be compared with the bibliography appended to another recent book on heredity which includes 426 titles from 170 authors. However, this is not intended as an adverse criticism of CASTLE'S excellent book, but is mentioned to show the limitations of its author's aims. Extensive literature lists are indispensable to students, but would defeat their own purpose in a book intended primarily for popular reading.

The press work is excellent and typographical errors are few, though "reversion" is rendered "revision" in the heading of chap. iv.—GEORGE H. SHULL.

NOTES FOR STUDENTS

The mycoplasma theory.—In spite of many attempts to establish the truthfulness or fallacy of ERIKSSON'S mycoplasma theory, its status has not been definitely settled, and it continues to be a subject of controversy. An outline of the history and the present status of the theory is presented by ERIKSSON[2] in a brief article occasioned by MARESCHKOWSKI'S[3] appropriation

[2] ERIKSSON, J., Über die Mykoplasmatheorie, ihre Geschichte und ihren Tagesstand. Biol. Centralbl. **30**:618–623. 1910.

[3] MARESCHKOWSKI, C., Theorie der zwei Plasmaarten als Grundlage der Symbiogenesis. Biol. Centralbl. **30**:278 ff. 1910.

of the term *mycoplasma* to designate one of the two types of protoplasm which he conceives to be the fundaments of which the organic world is built up. The article is a convenient historical summary but adds no new material to what has already been published. In it the author again calls attention to the fact, often emphasized by him, that the study of secondary rust pustules, as carried out by WARD and others, cannot have any bearing on the theory which is concerned only with the origin of the primary pustules. In concluding the author expresses a wish for a complete investigation of the whole problem.

ZACH,[4] in a paper dealing with the results of a cytological investigation of the pustules of *Puccinia graminis* and *P. glumarum*, comes to the conclusion that the mycoplasma theory is untenable and rests on a misinterpretation of the facts which, in themselves, he concedes are correctly described by ERIKSSON. ZACH studied microtome sections and free-hand sections of *P. graminis*, but only free-hand sections of fixed material of *P. glumarum*. From this material he describes processes of disorganization of the tissues. At the margin of the rust pustules the host cells have a turbid, deeply staining protoplasm which he identifies with ERIKSSON'S resting mycoplasma. The nuclei of these cells are much hypertrophied and seem to be filled with hyphae, some of which extend to the cell wall. The filaments degenerate and fuse into irregular lumps. The nucleus decreases in size and finally becomes an amorphous homogenous body termed an excretion product. Similar smaller bodies occurring throughout the cell he regards as identical with the "plasmanucleoli" of ERIKSSON. In more advanced stages the hyphae are largely dissolved, leaving only small amorphous particles. These processes, by which the cell and the parasite mutually destroy each other, resemble those formerly described by the author in his studies on the root tubercles of cycads. The process is termed phagocytosis, analogous to that phenomenon in animals. The figures accompanying the paper represent in a general way processes in cells undergoing disorganization as the result of the action of the fungi or other agents, which cause a slow dying of the cells. The "hyphae" figured bear not the least resemblance to the hyphae or haustoria of rusts.

In a criticism of the foregoing paper, ERIKSSON[5] points out that ZACH fails to state that he confined his studies to the primary uredo pustules, and furthermore that the pustules investigated by him were too far advanced to show stages of the mycoplasma, which is present only before the pustules become visible. The formations observed by ZACH belong to a later stage in the life of the rust. The various "excreted" bodies described by ZACH, ERIKSSON finds

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[4] ZACH, F., Cytologische Untersuchungen an den Rostflecken des Getreides und die Mycoplasmatheorie. Sitzungsb. K. Akad. Wiss. Wien Math.-Naturw. Kl. **119**:307–330. *pls. 2*. 1910.

[5] ERIKSSON, JAKOB, F. ZACH'S cytologische Untersuchungen über die Rostflecken des Getreides und die Mycoplasmatheorie. Sitzungsb. K. Akad. Wiss. Wien Math.-Naturw. Kl. **119**: pp. 8. 1910.

only in advanced stages of cell disorganization, and not during the mycoplasma stage. ERIKSSON also fails to find "hyphae" in the disorganizing nucleus, but believes the structures interpreted as such by ZACH to be chromatin threads.

A paper by BEAUVERIE[6] relates to the "plasmanucleoli" described by ERIKSSON. BEAUVERIE finds in the cells of fungi certain granules stainable with basic dyes, which he terms "corpuscules métachromatiques." In wheat plants attacked by rust he finds similar bodies in the mycelium, and in the host cells in the regions invaded by the fungus, but not in the normal cells. These granules he identifies with the plasmanucleoli of ERIKSSON. Just how giving these bodies a new name would, in itself, invalidate ERIKSSON's interpretation or constitute a new interpretation is not easy to see.

The solution of the problem which gave rise to the mycoplasma theory probably lies in the direction suggested by the recent work of PRITCHARD[7] on rust-infected grain seeds. PRITCHARD finds that rust-infected wheat seeds, to which little attention has been given from this viewpoint, contain living mycelium in the neighborhood of the rust sori. When such seeds are planted the fungus resumes its activity with the growth of the seedling, and penetrates both the stem and root of the young plant. It also grows in the spaces between the leaf sheaths. The formation of new uredo pustules from this mycelium has not been observed, nor have rusted wheat plants been obtained from infected seed grain under conditions rigorously excluding external infection.—H. HASSELBRING.

Spermatogenesis in Bryophytes.—WILSON[8] has completed his studies of spermatogenesis in *Mnium hornum* and also has investigated spermatogenesis in *Atrichum undulatum* and *Pellia epiphylla*. Because of the somewhat remarkable statements of J. and W. Docters VAN LEEUWEN-REIJNVAAN that centrosomes are constantly present in the spermatogenous cells in several species of *Polytrichum* and *Mnium*, and that in the ultimate division of these cells a reduction takes place whereby the haploid number of chromosomes is reduced to half (in *Polytrichum* to 3, and in *Mnium* to 4), these later divisions were studied with exceeding care.

In *Mnium hornum*, in the early stage of the penultimate division in spermatogenesis, a body is cut off by constriction from the nucleolus. In earlier divisions of the spermatogenous cells this division of the nucleolus was not observed. This body was never discovered outside of the nucleus and soon

[6] BEAUVERIE, J., L'hypothèse du mycoplasma et les corpuscules métachromatiques. Compt. Rend. **152**:612–615. 1911.

[7] PRITCHARD, F. J., The wintering of *Puccinia graminis Tritici* E. & H. and the infection of wheat through the seed. Phytopathology **1**:150–154. *pl. 1. fig. 1.* 1911. See also BOT. GAZ. **52**:169–192. *pl. 1.* 1911.

[8] WILSON, MALCOLM, Spermatogenesis in the Bryophyta. Ann. Botany **25**:415–457. *pls. 37–38. figs. 3.* 1911.

disappears. During prophase of the ultimate division of the spermatogenous cells, the nucleolus divides into two separate masses by constriction, and before separation is complete, a third small body buds off from one of the nucleolar bodies. These three bodies become free, but do not pass beyond the nuclear membrane, and the smallest one is considerably larger than is usually associated with centrosomes. These bodies were lost during later prophase, and their fate could not be determined. Chromosomes are constantly 6 in number and no difference in size could be observed.

The daughter nuclei at first contain several deeply staining granules, which later are replaced by a single centrally placed nucleolus. This nucleolus divides by constriction into two bodies, one of which again divides. The nuclear membrane then becomes indistinct, and two of the nucleolar bodies pass out into the cytoplasm, and probably increase by division, as more than two can often be found. Later they become rodlike and are usually grouped near a vacuole. At this stage the nucleus is barely distinguishable as a mass somewhat denser than the surrounding cytoplasm. The nucleolus may again cut off one or two bodies, which probably pass out into the cytoplasm and become associated with the rodlike bodies. These rods now increase in length, become irregularly curved, and look very much like chromosomes. Their number is usually three or four. This situation would seemingly explain the double reduction of J. and W. Docters VAN LEEUWEN-REIJNVAAN. The nucleolus now enters upon a third period of division, giving rise to two bodies which pass out into the cytoplasm, one being most likely the blepharoplast; the other WILSON thinks is perhaps the same as the "Nebenkörper" described in *Marchantia* by IKENO. All but one or two of the rodlike bodies now coalesce and form a spherical mass, which the author names the "limosphere." Later, when the limosphere is seen in optical section, it appears as a ring. In the last stages studied (the nearly mature sperms) the limosphere still persisted.

In *Atrichum undulatum* the sequence is much the same as in *Mnium*. No centrosomes could be found, and the chromosome number is 17. In *Pellia epiphylla*, centrospheres and perhaps centrosomes are present in later divisions in the antheridium. The author thinks the blepharoplast may be derived from the centrosome. A limosphere and accessory body are present in the sperm, but their origin was not determined.

WILSON'S work gives evidence of extremely careful study, and seems to furnish a satisfactory explanation for the fantastic performances which have been reported as taking place during spermatogenesis in Musci.—W. J. G. LAND.

Origin of the mitotic figure.—LAWSON'S[9] study of the microspore mother cells of *Disporum*, *Gladiolus*, *Yucca*, *Hedera*, and the vegetative cells in the root tip of *Allium* has revealed a series of stages in the development of

[9] LAWSON, A. ANSTRUTHER, Nuclear osmosis as a factor in mitosis. Trans. Roy. Soc. Edinburgh **48**:137–161. *pls. 1–4.* 1911.

the mitotic spindle which have never before been described. These new stages are to be found in the prophase immediately preceding the organization of the equatorial plate, and concern the fate of the nuclear membrane. Many authors have either described or figured the breaking down of the nuclear membrane at a time when the multipolar stage has been reached, or in vegetative cells when the polar caps have been completely formed. Contrary to the generally accepted view, LAWSON finds that the nuclear membrane does not break down or collapse at any period during the spindle development, but behaves as one would expect a permeable plasma membrane to behave under varying osmotic relations.

The nucleus is regarded as an osmotic system, and its membrane constitutes an essential element in that system. As the prophase proceeds, the nucleus or the nuclear vacuole, as he calls it, becomes smaller and smaller, and the membrane gradually closes in about the chromosomes, which later become crowded together around the nucleolus. When the karyolymph becomes so much reduced that it is no longer visible as a clear nuclear sap, the membrane becomes closely applied to and completely envelops the surface of each chromosome. As a consequence, instead of a single osmotic system represented in the nucleus, there have been established now as many independent osmotic systems as there are chromosomes.

The gradual diminution of the nuclear vacuole brings about a condition where a limited amount of cytoplasm of reticulate structure is obliged to occupy a space which has greatly increased by the reduction in volume of the nuclear vacuole. This necessarily sets up in the cell a tension sufficient to cause a readjustment and a changed configuration in the reticulate form of the cytoplasm, and therefore the cytoplasm in the region of the nuclear wall, drawn out from the reticulum by the receding membrane, becomes changed to the form of fine threads or fibrils of the "kinoplasm." The lines of tension are constantly shifting throughout the prophase. Such a shifting does not mean the changing of the threads bodily from one position to another, but it means the relaxing of the tension along certain threads, which would consequently fall back into the reticulate forms, and the setting up of new lines of tension by the drawing out of threads from the hitherto undifferentiated reticulum. Thus not only individual threads, but entire cones of fibrils may appear to assume different positions. The attachment of the spindle fibrils to chromosomes is brought about by the enveloping of each chromosome by the receding membrane.

Taking all the stages observed into consideration, the author concludes that the achromatic spindle in vascular plants is simply an expression of a state of tension in the cytoplasm, and that this tension is caused in the first place by nuclear osmotic changes that create a condition where a limited amount of cytoplasm is obliged to occupy an increased space. Thus, he regards the achromatic figure as not an active factor in mitosis, but nothing more than a passive effect of nuclear osmotic changes.—S. YAMANOUCHI.

The fossil conifers of Spitzbergen.—An important contribution by GOTHAN[10] contains a description of the fossil woods of various geological horizons from the island of Spitzbergen, brought back for the most part by Arctic expeditions during the past 50 years. The most interesting woods from the evolutionary standpoint are those from the Upper Jurassic of Green Harbour, Esmarks Glacier, and Wimansberg. Of these the author remarks: "Es ist überhaupt gemein auffallend, wie häufig man in der Hoftüpflung zahlreicher Hölzer der oberen Juraformation des Nordens Araucarioiden Charackteren begegnet, und dies bei Angehörigen von Familien, die mit den Araucarieen im übrigen sicher weiter nichts zu thun haben" (p. 18). The author holds that strongly pitted rays, together with normal or traumatic resin canals in the wood, are an infallible indication of abietineous affinities. Since most of the woods which he describes in this memoir have these characteristics, he puts them with the Abietineae, in spite of the fact that other apparently more important features are clearly araucarian. It is interesting to note in this connection that SEWARD[11] has referred woods of a similar type from the Upper Jurassic of Yorkshire in England to araucarian affinities. There seems little reason to doubt that SEWARD rather than GOTHAN is right in this matter, especially as it appears from recent studies on the living Araucariineae, as yet unpublished, that these came from ancestors which, on comparatively anatomical evidence and in accordance with generally accepted morphological principles, possessed bars of Sanio in their tracheids, wood parenchyma, opposite pitting, resin canals in the wood, strongly pitted rays, and a clearly double system of ovulate cone scale bundles, all characters unmistakably abietineous. It is accordingly not surprising to find intermingled araucarian and abietineous characters in the araucarian woods of the Jurassic. Moreover, if one admits that GOTHAN's jurassic woods are in reality abietineous and not araucarian, a grave difficulty arises in the case of recently described woods from the American Cretaceous, such as *Brachyoxylon*, *Araucariopitys*, *Paracedroxylon*, etc., which sometimes have ligneous resin canals and sometimes lack them, and likewise have both the araucarian and the abietineous types of ray, the former being more abundant in these later woods. The facts can all be squared with a derivation of the Araucariineae from the Abietineae, but not with the reversed derivation. The most interesting of the new genera and species described in this memoir are *Protopiceoxylon* (*P. extinctum*, apparently beyond question araucarian), *Protocedroxylon* (*P. araucarioides*), and *Cedroxylon* (sic!) *transiens*. It seems quite clear from this and other publications of GOTHAN on the Jurassic woods of northern Europe that the Araucariineae were at that period not very remote from their abietineous source. It follows

[10] GOTHAN W., Die fossilen Holzreste von Spitzbergen. Kung. Svensk. Vetensk. Handl. **45**: no. 8. 1910.

[11] British Museum catalogue of Mesozoic plants, Jurassic flora. II. Liassic and Oolitic floras of England. *pls. 6, 7*. London. 1904.

that the so-called Araucarioxyla of the earlier Mesozoic have nothing to do with the evolution of the stock from which *Agathis* and *Araucaria* have been derived. *Walchia* and *Voltzia* from the Permian and Trias, moreover, do not present the *Araucarioxylon* type of wood. The situation thus becomes difficult indeed for those who believe the Araucariineae to be the oldest conifers, and to constitute the articulation of the family with the Cordaitales.—E. C. JEFFREY.

Cytology of the Chytridineae.—BALLY,[12] working in STRASBURGER'S laboratory, has added much of importance to our knowledge of the cytology of the Archimycetes. In *Synchytrium taraxaci* the primary nucleus divides, not by mitosis as in *S. decipiens* and *S. puerariae*, which have been investigated by STEVENS and KUSANO, but by a process analogous to nuclear gemmation, in which masses of chromatin originally derived from the nucleolus pass into the cytoplasm as chromidia which later become the basis of the secondary nuclei. While the stages in this process are not fully worked out, there can be little doubt from the figures showing the old primary nucleus still undivided, together with scores of secondary nuclei in the same parasite, but that the description given is substantially correct. These nuclei later divide by mitosis and always have four chromosomes. Curiously enough the conspicuous asters ("karyodermatoplasts") which reconstruct the nuclear membrane in *S. decipiens* and *S. puerariae* appear to be absent from *S. taraxaci*.

BALLY does not follow PERCIVAL[13] in including *Chrysophlyctis* in *Synchytrium*, but he fully confirms and substantiates PERCIVAL'S account of the remarkable amitoses in the resting sporangia of that plant. Here nuclear gemmation reaches its climax. The extruded chromidia never organize secondary muclei, but pass unchanged into the zoospores, which are formed in a most peculiar manner, while the remains of the primary nucleus still persist undivided in the center. Here again more details would be very welcome, but it is clear from the figures, together with those of PERCIVAL, that there is something here far different from the ordinary behavior of nuclei, or better of chromatin, for such cysts may be said to have no nuclei, though rich in chromatin.

In *Urophlyctis Rübsaamenii*, amitosis, largely by nuclear gemmation of which figures showing details are presented, appears to be the sole method of nuclear multiplication. The cytological condition of this plant contrasts sharply with that of the two preceding, in that the parasite becomes coenocytic with the beginning of growth. On the basis of such differences he separates the Archimycetes into two series: one essentially uninucleate, including *Synchytrium* and *Chrysophlyctis;* the other coenocytic from almost the beginning, including the Cladochytriaceae, and more doubtfully the Rhizidiaceae

[12] BALLY, WALTER, Cytologische Studien an Chytridineen. Jahrb. Wiss. Bot. **50**:95–156. *pls. 1–5. figs. 6.* 1911.

[13] PERCIVAL, JOHN, Potato wart disease: the life history and cytology of *Synchytrium endobioticum* (Schilb.) Percl. Centralbl. Bakt. **25**:440–446. *pls. 1–3.* 1910.

and Olpidiaceae, with perhaps also the Hyphochytriaceae. He follows PAVILLARD in believing that the Synchytriaceae show most similarity in cytology to the Sporozoa, and were probably derived from them, but he does not commit himself to any opinion concerning the origin of the second group. —ROBERT F. GRIGGS.

Movement of water.—The ascent of water in vessels containing chains of water and air bubbles (Jamin's chain) may take place in one of two ways: either the whole chain moves upward or the water alone moves while the air bubbles are stationary. SCHAPOSCHUIKOFF[14] claims that the physical conditions of a Jamin's chain in the conducting vessels of plants are not such that they prevent the movement of the chain as a whole. Reasoning theoretically, he concludes that the presence of cross walls in the vessels do not hinder such a movement. The bubble just above the cross wall and the one just below are under unequal pressures, the former under reduced pressure owing to the suction from above, and the latter under increased pressure owing to the rise of water below. On account of the increased pressure the bubble below goes into solution, passes through the cross wall, and separates out again under the reduced pressure above. It is assumed that the bubbles arise only from gases dissolved in the water filling the vessel. They separate out when the water consumption by the plant is greater than the supply, causing a reduced pressure in the vessels.

The author constructed a very ingenious apparatus to put the above theoretical conclusions to the test of experimental proof. In his apparatus gas bubbles began to form from the gases in solution when the pressure reached one-half to one-third of an atmosphere in a glass tube corresponding to a conducting vessel in the plant. As soon as a gas bubble reached the cross wall, the filtration of water through the membrane ceased. The manometer soon showed an increased pressure in the tube, due to the continued rise of water from below. After a short time the bubble went into solution and passed through the water-saturated membrane, allowing the filtration of water to continue. The manometer now showed a sinking of pressure again. The passage of the bubbles by the sculpturing of the wall may be explained in a way similar to their passage through the cross walls. As soon as a bubble is held by a thickening in the wall, unequal pressures are set up, causing it to dissolve sufficiently to pass on.—CHAS. O. APPLEMAN.

Chaparral.—A woodland consisting of stunted trees, seldom more than 10 feet, and apparently a response to the peculiar conditions of Southern California, has been studied by PLUMMER,[15] and a report made upon its impor-

[14] SCHAPOSCHUIKOFF, WALK., Sollen die Luftblässchen der sogenannten Jaminschen Kette in den Leitungsbahnen der Pflanzen für immobil gehalten werden? Beih. Bot. Centralbl. **27**:438–444. *figs 2*. 1911.

[15] PLUMMER, FRED G., Chaparral. U.S. Dept. Agric., Forest Service, Bull. 85, pp. 48. 1911.

tance in conserving moisture and regulating the flow of streams in a region where the water supply is of the utmost economic importance. This conservation is accomplished by the root system penetrating the soil and assisting percolation, while at the same time the trees prevent erosion by shading the ground, by breaking the force of hot winds, and by lessening evaporation. The most active destructive agent is fire, which rapidly sweeps the half-dry vegetation from the arid mountain slopes. The investigator offers good arguments in support of his belief that the protection of the chaparral cover is of great importance in preventing the loss of water needed for irrigation.

From the ecological viewpoint, the "true chaparral," which seems to be a climatic formation holding complete possession of its domain and found principally in California, is distinguished from "mock chaparral," which is a pioneer association of similar dwarfed trees occurring in the forest succession in parts of Arizona, New Mexico, Colorado, and Utah. In both the same genera and often the same species of sclerophyllous trees are to be found. The dominant members are various species of *Adenostoma*, *Arctostaphylos*, *Ceanothus*, and *Quercus*, while forms of *Rhus*, *Cercocarpus*, *Rhamnus*, and *Ribes* are among those of secondary importance.

The study includes a consideration of the ecological relations and relative economic importance of the more abundant species, of the methods of controlling fires, of restocking after fires, and of the possibility of introducing larger tree species. A map shows the distribution of this interesting forest formation in California.—GEO. D. FULLER.

Stems of Diplolabis and Metaclepsydropsis—GORDON[16] has described the hitherto unknown stems of *Diplolabis Römeri* and *Metaclepsydropsis duplex*, as well as the attachment and vascular supply of their leaves. The stem in both species is a long dichotomous rhizome, with nodes only at wide intervals. The stele, circular in section, is in *Diplolabis* composed entirely of tracheids, while in *Metaclepsydropsis* there is much parenchyma scattered among the small central xylem elements. The leaf trace departs in each case as an elliptical strand with two lateral mesarch protoxylems. In the lower portion of its course, it may resemble in turn the petiolar bundles of *Clepsydropsis*, *Dineuron*, or *Zygopteris;* but after its entrance into the petiole it assumes, respectively, the typical "H" of *Diplolabis* and the "dumb-bell" of *Metaclepsydropsis*. The changes in structure presented by the foliar bundle as it ascends from node to petiole, and the striking similarity at the base of the leaf trace between these two species, and indeed among all the Zygopterideae, furnish further evidence of the conservatism of this region and of its importance as a seat of ancestral characters.—E. W. SINNOTT.

[16] GORDON, W. T., On structure and affinities of *Diplolabis Römeri* (Solms). Trans. Roy. Soc. Edinburgh **47**[1]:711–736. *pls. 1–4.* 1911.

———, On the structure and affinities of *Metaclepsydropsis duplex* (Williamson). Trans. Roy. Soc. Edinburgh **48**[1]:163–190. *pls. 1–4.* 1912.

Anatomy of Osmundites.—SCHUSTER[17] has described the anatomical structure of a new species of *Osmundites* (*O. Carneri*) from Paraguay. He considers it an "ectophloic siphonostele," and calls especial attention to the absence of leaf gaps. A ring of xylem, unbroken but very thin opposite the wide "rays," is figured in a text diagram, but it is noteworthy that the attachment of leaf trace to stele has not been drawn. The plates of photographs, however, show broad and indisputable leaf gaps formed by the departure of leaf traces which are thin and arched from the very first. The preservation of tissues other than the xylem is not good enough to determine the presence or absence of internal phloem, but the wide gaps and other striking resemblances between the stele of this species and that of *Osmundites skidegatensis*, where internal as well as external phloem is well developed, would lead one to suspect very strongly the existence of this tissue in *O. Carneri*. There is doubt as to the horizon of the new species, but its author places it as probably Tertiary, though possibly Jurassic. Species of *Osmundites* have now been described from the continent of Europe, western Canada, Paraguay, South Africa, and New Zealand.—E. W. SINNOTT.

Respiration and wounding.—SCHNEIDER-ORELLI[18] finds that wounding apples, pears, and potatoes which are no longer capable of forming wound periderm increases the amount of carbon dioxide given off by such fruits and tubers above that normally given off. He concludes, therefore, that the increased respiration is due to wounding alone, and not to renewed cell division which follows wounding in tissues which are still capable of growth. An attempt to apply the same idea to the study of the stimulation of respiration due to infection by fungi gave no results, since it was impossible to separate the carbon dioxide produced by the fungus from that produced by the host.—H. HASSELBRING.

A glucoside.—Saponarin, a glucoside of the formula $C_{21}H_{24}O_{12}$, has been found in 24 species of phanerogams (8 families) out of more than 1300 species examined. It is contained in the epidermis of leaves and stains blue to violet with IKI. MOLISCH[19] now finds it in *Madotheca platyphylla*, the only liverwort out of 36 species examined. Its peculiar distribution in the plant kingdom and its liability of being mistaken for soluble starch make it of interest. It should be stated that the writer's microchemical methods do not prove that this substance is saponarin.—WILLIAM CROCKER.

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[17] SCHUSTER, J., *Osmundites* von Sierra Villa Rica in Paraguay. Ber. Deutsch. Bot. Gesells. **29**:534–540. *pls. 2*. 1911.

[18] SCHNEIDER-ORELLI, O., Versuche über Wundreiz und Wundverschluss an Pflanzenorganen. Centralbl. Bakt. II. **30**:420–429. 1911.

[19] MOLISCH, HANS, Über das Vorkommen von Saponarin bei einen Lebermoos (*Madotheca platyphylla*). Ber. Deutsch. Bot. Gesells. **29**:487–491. 1911.

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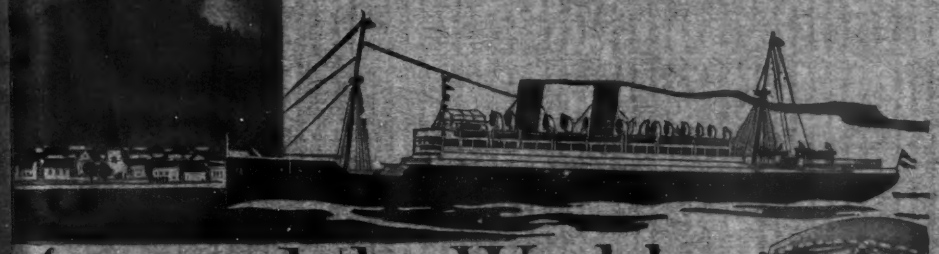

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